

Exemplarising the Origin of a Science

A Path to Genetics: From Mendel to Bateson

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I, Yafeng Shan, confirm that the work presented in this thesis is my own.
Where information has been derived from other sources, I confirm that
this has been indicated in the thesis.

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Abstract

This thesis aims to propose and defend a new way of analysing and understanding the origin of genetics (from Mendel to Bateson). Traditionally philosophers used to analyse the history of genetics in terms of theories. However, I will argue that this theory-based approach is highly problematic. In Chapter 1, I shall critically review the theory-driven approach to analysing the history of genetics and diagnose its problems. In Chapter 2, inspired by Kuhn's concept "exemplar", I shall make a new interpretation of exemplar and introduce an exemplar-based approach. Before introducing my exemplar-based analysis, I find it necessary to scrutinise the origin of genetics from Mendel to Bateson. In Chapter 3, I shall reinterpret Mendel's work on *Pisum* by re-examining Mendel's paper (1865) and its historical research context. In Chapter 4, by carefully examining the conceptual changes, I argue that the rediscovery event in 1900 should be better characterised as attempts of incorporating Mendel's work with the work of "rediscoverers" (i.e. de Vries, Correns, Tschermak, and Bateson) rather than a mere reintroduction to Mendel's work. In Chapter 5, I shall use the exemplar-based approach to analysing and interpreting the origin of genetics from Mendel to Bateson. In Chapter 6, I shall defend my exemplar-based characterisation of the origin of genetics by dismissing the potential responses from the theory-driven one, critically examining a potential mechanism-based analysis, and making the further notes on the implication of taking the exemplar-based approach to investigate scientific practice.

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Introduction

The Practical Turn in the Philosophical Examination of History of Science

History of science has been important for philosophers of science. Philosophers were interested in reconstructing the history of sciences to study the nature and pattern of the development of science: Is the development of science progressive through the history? Is the history of science a cumulative and continuous progress? In addition, considering that science has been a highly successful knowledge-gaining enterprise, philosophers used to believe that a careful examination of the history of science sheds light on many central problems in philosophy of science, or even in more general philosophy. For example, the question of whether the development of science is continuous was central to the scientific realism/antirealism debate. (Hardin & Rosenberg, 1982; Laudan, 1981; Leplin, 1981). Moreover, some philosophers (for example, Lakatos, 1970) even contended that historians could and should learn from the philosophical reconstruction of the history of sciences. In short, history of science has been one of the central topics in the contemporary philosophy of science.

In the past three decades, there has been an ongoing change to the focus of the philosophical examination of the history of science. Traditionally philosophers of science focused attention on scientific knowledge. The history of science, according to this traditional approach, is often depicted as a history of scientific knowledge, though there are overwhelming disagreements in the literature on the nature,

structure, dynamics and interrelation of scientific knowledge in the history. In this regard the question of how best to characterise scientific knowledge was widely discussed. In particular, some argued that it was best characterised in terms of theories (Popper, 1959), paradigms (Kuhn, 1962, 1970b), research programmes (Lakatos, 1968, 1978), disciplines (Toulmin, 1972), research traditions (Laudan, 1977), or fields (Darden & Maull, 1977). It was also debated whether the interrelation of successive bodies of scientific knowledge is reduction (Nagel, 1961), comparable replacement (Popper, 1959), incommensurability (Feyerabend, 1962; Kuhn, 1962), or explanatory extension (Kitcher, 1984, 1989).

Despite these disagreements, scientific theories were once widely considered to be a best candidate to reflect and represent scientific knowledge and its development. As Frederick Suppe puts it, "theories are the vehicle of scientific knowledge." (Suppe, 1977, p. 3) It should be noted that this theory-based understanding of scientific knowledge does not merely refer to the doctrine that scientific knowledge should be equated with theories. For example, Karl Popper once claimed that "[t]he empirical sciences are systems of theories. The logic of scientific knowledge can therefore be described as a theory of theories." (Popper, 1959, p. 37) In addition, many philosophers (for example, Lakatos, 1968; Laudan, 1977), although rejecting the claim that scientific knowledge are just theories, still believed that theories are fundamental components of scientific knowledge. For example, Larry Laudan, who was well known for analysing the history of scientific knowledge in terms of research traditions, still identifies that "[e]very research tradition has a number of specific theories which exemplify and partially constitute it." (Laudan, 1977, p. 78) Accordingly, scientific changes (e.g. the Copernican revolution and the Chemical revolution) have also been widely characterised as shifts from one theory to another, though the relation of two successive theories is under debate. (Nagel, 1961; Popper, 1959) All these philosophical treatments are implicitly rooted in a consensus among many philosophers of science before the 1980s¹: *Scientific knowledge and its development is best characterised and structured by theories.*

¹ Nevertheless, this consensus was still influential after 1980s. (For example, Gardenfors & Zenker, 2013; Rivadulla, 2004; Sterelny & Griffiths, 1999; Vance, 1996)

This consensus underlies a popular “theory-driven” approach in the philosophy of science, which is perfectly summarised by C. Kenneth Waters:

Philosophers (perhaps I should say we) typically analyze scientific knowledge by identifying central explanatory theories. Then for each theory, we analyze its central concepts and principles (or laws), detail how it can be applied to explain the phenomena, reconstruct how it is justified, explore how it might be further developed or how its explanatory range might be extended (the so-called ‘research program’), and consider how it should be interpreted (for example, instrumentally or realistically). (Waters, 2004, p. 784)

In short, the theory-driven approach assumes the centrality of the role of theory in science, and guides philosophers to articulate the nature, structure, and implications of scientific knowledge in terms of theories. In addition to be applied to characterise scientific knowledge and its history, this approach is well illustrated in many discussions in philosophy of science. The problem of demarcation of science from pseudoscience had been a question of whether a theory is falsifiable. The debate between scientific realism/antirealism is typically portrayed as the questions of whether certain terms in scientific theories refer to mind-independently objects and of whether scientific theories are (at least approximately) true. Relativism is traditionally understood as the view that choice in scientific change has no “rational” basis. Even today, it is still a fact, as Ronald Giere points out, that “so many topics in contemporary philosophy of science continue to be framed in terms of theories.” (Giere, 2000, p. 515)

Before evaluating this approach, I find it necessary to briefly clarify what a theory is for philosophers. A scientific theory is conventionally thought to be a corpus of statements, which explains the phenomena in the empirical world by employing concepts, hypotheses, and principles (or laws). For example, the theory of Newtonian mechanics consists of Newton’s three laws of motion and the law of gravitation by employing the concepts like force, velocity, etc. Among various interpretations, there are two dominant philosophical analyses of scientific theories.

One is the syntactic view² (also once called the received view). According to this view, a scientific theory is a set of statements, which can be reformulated into a deductive axiomatised system written in first-order logic.³ The other is the semantic view (for example, Suppe, 1989; Suppes, 1967; van Fraassen, 1980), which construes scientific theories as extralinguistic entities in terms of families of models. A model is a mathematical structure that satisfies a theory, though there is still no consensus on what a mathematical structure is. Some (for example, da Costa & French, 1990; Suppes, 1967) identify models as set-theoretical structures⁴, while other (van Fraassen, 1980, 1989) regard models as state-space structures⁵. Although even now no agreement on the nature or interpretation of scientific theories has been forthcoming, it has become a canonical problem in the 20th century philosophy of science. As Suppe observes, “If any problem in the philosophy of science justifiably can be claimed the most central or important, it is that of the nature and structure of scientific theories... It is only a slight exaggeration to claim that a philosophy of science is little more than an analysis of theories and their roles in the scientific enterprise.” (Suppe, 1977, p. 3) No matter what a scientific theory should be best represented as, this debate itself is an instantiation of the theory-driven approach. If the role of theory is not so important in understanding science and its history, why is there so much discussion on the nature of a scientific theory?

However, the theory-driven approach has been criticised by many philosophers in the 1980s and 1990s. Firstly, the theory-driven approach overlooks the significance of experiments and other non-theoretical aspects in science. (*The Problem of Practice*) As Ian Hacking points out, “Philosophers of science constantly discuss theories and representation of reality, but say almost nothing about experiment,

² Classical statements of the syntactic view can be found in Braithwaite (1953), Hempel (1965), and Nagel (1961).

³ Carnap was explicit on the point that if a theory does not admit of a reformulation satisfying the conditions of the syntactic view, it is not a genuine scientific theory. (Carnap, 1963, pp. 422–423)

⁴ According to this definition of model, a scientific theory is a mathematical structure defined via the language of set theory.

⁵ According to this definition of model, a theory is a state-space structure which represents the behaviour of all physical systems that are idealised replicas of phenomena within the scope of the theory. If the theory has n parameters, then the state-space is an n -dimensional space. The behaviours of the physical systems are represented by various configurations imposed on the state space.

technology, or the use of knowledge to alter the world.” (Hacking, 1983, p. 149) Many (for example, Cartwright, Schomar, & Suárez, 1995; Hacking, 1983) feel dissatisfied with this misleading approach. One lesson that can be learnt from these criticisms is that the history of science, even if from a philosophical perspective, should be much more than a history of scientific theory.

Secondly, the traditional consensus that theories are carriers of scientific knowledge about the empirical world has also been challenged.⁶ (*The Problem of Theories as Vehicles of Scientific Knowledge*) Some suggest that it is that models⁷ rather than theories represent what happens in the empirical world. As Nancy Cartwright argues, “[F]undamental theory represents nothing and there is nothing for it to represent. There are only real things and the real ways they behave. And these are represented by models, models constructed with the aid of all the knowledge and techniques and tricks and devices we have. Theory plays its own small important role here. But it is a tool like any other; and you can not build a house with a hammer alone.” (Cartwright et al., 1995, p. 140) As we shall see, both these reactions highlight a gradual shift of the focus of the philosophical analysis of science, and correspondingly influence the philosophical examination of the history of science.

Thirdly, these theory-driven analyses of the history of science overlook one significant aspect of scientific theory: the construction and development of a theory.⁸ (*The Problem of Theory Construction*) As Kuhn once insightfully points out, “[Philosophy of science] is comparatively little concerned with the temporal development of theory.” (Kuhn, 1977b, p. 14) In particular, despite the importance of theory in the analysis of the history of science, philosophers seem to forget to

⁶ Although Kuhn (Kuhn, 1970b, p. 181) already argued that the conventional understanding of a theory failed to represent scientific knowledge “in nature and scope”, this early examination of theories as vehicles of scientific knowledge was not taken seriously at that time.

⁷ Note that “models” in this context are not what constitute the theories as defined in the semantic view.

⁸ It should be highlighted that the neglect of the problem of the construction and development of a theory is not a logical consequence of taking the theory-driven approach, but the philosophers of science who take the theory-driven approach do pay insufficient attention to investigating the construction and development of a theory.

study how a theory is established and constructed.⁹ As Norwood Russell Hanson emphasises, “The issue is not theory-using, but theory-finding.” (Hanson, 1958, p. 3)

Given these problems, newer philosophical approaches in analysing the history of science shift attention from scientific knowledge to scientific practice¹⁰, from theories to theorising, from concepts to conceptual practices; and even when the discussion is restricted to scientific knowledge, there is a shift from theoretical knowledge (know-that) to practical knowledge (know-how). In short, for many philosophers (for example, Chang, 2014, p. 67; Giere, 2011, p. 61; Soler, Zwart, Lynch, & Israel-Jost, 2014, pp. 21–22; Waters, 2014, p. 121), the central issue has shifted from what scientists find out to how scientists find out. This is the so-called practical turn in the philosophy of science.

Correspondingly several philosophical accounts of the history of science with a more rigorous practice-based approach were proposed. Philip Kitcher (1984) characterises the history of science in terms of practices, while Hacking (1992, 1994), building on the work of the historian A.C. Crombie (1994, 1996), develops the notion of styles of scientific thinking to understand the history of science. Another two more recent contributions are Lindley Darden’s mechanism-based account of the history of biology (Craver & Darden, 2013; Darden & Craver, 2002; Darden, 2005), and Hasok Chang’s analysis of the history of chemistry in the 18th and 19th century in terms of systems of practice (Chang, 2012).

The Context of Discovery, Theory-Construction, and the Origin of a Science

If the focus of the old philosophical examinations of the history of science is the history of scientific knowledge before the practical turn, then that of current philosophical analysis can be understood as the history of scientific practice.

⁹ It is worth noting that Kuhn, though well realising this problem and advocating paradigm as an alternative to theory to analyse the history and practice of science, still said little on the establishment of a paradigm. See the discussion in Chapter 2.

¹⁰ In fact, the shift can already be found in many pre-1980 works. There are some non-theoretical elements in the elucidation of paradigms, research programmes and research traditions. However, the significance of the shift was not universally recognised until 1980s. It should also be noted that the distinction between scientific knowledge and practice is not sharp. Scientific knowledge includes practical know-how, while scientific practice relies on some theoretical knowledge.

Nevertheless, I still find that these philosophical analyses pay insufficient attention to a very important question, the origin of an established school of scientific practices.¹¹ How is a school of scientific practice first established? What is a best way to analyse and characterise the origin of a school of scientific practice? This is an area, traditionally conflated with “the context of discovery”¹², despised by philosophers. Discovery was contrasted with justification as the two main activities of scientists. Philosophers of science once widely accepted that there is a sharp distinction between the process of how scientists propose a theory and the method of justifying it. Moreover, they claimed that the former is not a topic for philosophers.

The initial stage, the act of conceiving or inventing a theory, seems to me neither to call for a logical analysis nor to be susceptible of it. (Popper, 1959, p. 7)

The solution of these historical problems involves the individual psychology of thinking and the sociology of thought. None of these questions are our business here. (Braithwaite, 1953, pp. 20–21)

In fact, how a theory is constructed is much more important and complicated than philosophers used to think. Theory construction involves an intertwined practice of conceptualisation, modeling, testing, modification, confirmation, and so on. So it cannot be simply identified with a process of how an idea occurs to a scientist. As Darden points out, “A theory rarely, if ever, arises all at once in a complete form. Vague ideas about postulated explanatory factors may take on more form as new data are found and new theoretical components added. A negative result may produce a change in only one part of a theory, with subsequent modification incorporating new ideas, which fit the data better. Connections to empirically confirmed items in another field may be important

¹¹ Craver and Darden’s work (Craver & Darden, 2001, 2013; Darden & Craver, 2002; Darden, 2002, 2006a) is definitely an exception.

¹² There is a difference between the origin of a school of scientific practice and the context of discovery. The process of discovery is construed as an intellectual act, while the origin of a school of scientific practice is a more complex multi-faceted development. However, it should be noted that the philosophical understanding of the development of a science is conflated with the history of a theory. Thus, strictly speaking, there is very few serious philosophical articulation of the origin of a science until Darden’s paper (1980).

in constructing part of a theory and at the same time bring a measure of justification.” (Darden, 1980, p. 152) The neglect of theory-construction in philosophy of science is particularly well reflected in the case of the early development of genetics. Although since the 1980s historians have done much important work on the early period of the history of genetics (for example, Bowler, 1989; Kohler, 1994; Olby, 1985), philosophers of science were yet to draw on the fruitful wealth of historical work which has been done. On the one hand, few philosophers took serious attempts to study the development of early genetics. On the other hand, as I shall show in Chapter 1, most of philosophical works on the history of genetics in the 1980s and 1990s relied on a superficial understanding of the history.

In response, Darden (1980, 1991, 2006a) made a substantial contribution to this neglected topic by articulating the development of the theory of genetics from 1900 to 1926. Despite this, the philosophical examination of the origin of genetics remains largely overlooked by philosophers. Moreover, given the practical turn, as I shall show in the section 1.2, Darden’s analysis of theory-construction in genetics is insufficient to reflect the multifaceted development of early genetics. In particular, Darden’s analysis is still mainly on the theoretical aspect of the development of the early period of genetics. However, as I shall show, the construction of the non-theoretical aspect (e.g. how to set up an experiment and how to define a research problem) is also worth articulating. In other words, a more comprehensive articulation of the origin of genetics is necessary. This is the primary motivation of this thesis.

In addition, many of the philosopher’s analyses of the history of scientific practice¹³ oversimplify or distort the actual history and overlook the historical context. This is why Leslie Pearce Williams once strongly opposed the philosophical reconstruction of the history of science:

It is time, now, to comment on the title of this essay review. [i.e. Should philosophers be allowed to write history?] I mean the question quite

¹³ However, some works, like Chang’s works (2004, 2012), are definitely exempt from this charge.

seriously and I shall now answer it with a resounding ‘NO!’ Let me generalise at my own peril. Philosophers tend to be interested in ideas, their logical connections and their logical consequences. They do not seem to find it very interesting to ask where ideas came from, how they developed, and how they were interpreted by others who claim to have been influenced by them. (Williams, 1975, p. 252)

Although Williams’s hostility aimed at the works of logical empiricists and critical rationalists in the 1960s and 1970s, his objection is still applicable to many recent philosophical examinations of the history of science. Quite a few philosophical accounts of the history of science still rely on a very superficial and incomplete understanding of the actual history. As I shall show in 1.2 and 1.3, the philosophical examinations of the history of genetics are good examples. Philosophers have different foci from historians, but philosophers have to pay serious attention to the problems of the formation, development, and representation of scientific practice in its historical context. It is a fair point that many contemporary philosophers of science still fail to sufficiently follow and benefit from cutting-edge research by historians of science, especially in the case of the history of genetics. My second motivation of this thesis is to provide a philosophical analysis of the history of genetics with a more solid understanding of the history.

Thus, my ultimate concern in this thesis is to explore a new way to analyse and understand the origin of a particular school of scientific practice, namely, genetics. Methodologically speaking, my thesis will be located in an ongoing movement called integrated history and philosophy of science¹⁴, which encourages a plurality of approaches to understanding science by blending philosophical analysis and historical interpretation (Arabatzis & Howard, 2015, pp. 1–2). In Chapter 1, I shall review a number of philosophical analyses of the history of genetics, and show in what sense the approach underlying these analyses is theory-driven. I will then diagnose its problems and weaknesses. In Chapter 2, on the basis of the examination of Kuhn’s novel notion “exemplar”, I shall provide a new interpretation of exemplar and propose an exemplar-based approach to understand and analyse

¹⁴ For the contemporary state of integrated history and philosophy of science, see Schickore (2011), Arabatzis and Schickore (2012),

the history (especially the origin) of a science. Before introducing an exemplar-based analysis, I shall begin with a historical re-examination of the origin of genetics. In Chapter 3, I shall carefully revisit Mendel's research within its historical context (especially the influence of Gärtner's work) to strengthen the view that Mendel's concern and research is about developmental series of hybrid progeny. Based on my new analyse of Mendel's work on *Pisum*, in Chapter 4, I shall further delve into the historical analysis of the rediscoverers' work, and attempt to reveal the actual development and incorporation of Mendel's work with the study of heredity at the turn of the twentieth century by examining the differences of the conceptual framework of the rediscoverers. In Chapter 5, given my historical interpretations of early Mendelian genetics, I shall show how my exemplar-based approach can be used to analyse the origin of genetics, and argue that my exemplar-based one is better fit than the old theory-driven one. In Chapter 6, I shall examine some potential responses and challenges from the theory-driven approach, critically examine a potential mechanism-based account of the origin of genetics, and make some further notes on the exemplar-based approach.

1

The Theory-Driven Approach, the Theory-Centric View, and the Philosophical Analyses of the History of Mendelian Genetics

In this chapter, I aim to critically examine the problems of the traditional philosophical accounts of Mendelian Genetics. Firstly, I shall provide a brief summary of the history of Mendelian genetics. Secondly, after reviewing some typical theory-driven accounts of Mendelian genetics, I shall articulate the problems of the theory-driven approach to analysing the history of Mendelian genetics. Thirdly, by developing Waters' criticisms of the theory-driven approach, I shall make a detailed critical examination of the assumption of the theory-driven approach, namely, the theory-centric view.

1.1 Philosophy and the History of Genetics

In Introduction, I have briefly argued that the theory-driven approach was influential in the philosophical examination of the history of science. A good example is the debate on theory reduction in genetics, one of central topics in the

philosophy of biology in the period 1970s-1990s. With the great impact of the discovery of the structure of DNA in 1953, it seems natural for many philosophers (for example, Goosens, 1978; Hull, 1979; Ruse, 1976; Schaffner, 1976) to distinguish the history of genetics chronologically with two episodes: Mendelian genetics and molecular genetics. Thus, the philosophers began exploring the nature of the shift from Mendelian genetics to molecular genetics. Since the late 1960s¹⁵, the question of whether the theory of Mendelian genetics is reducible to the theory of molecular genetics has been one of the most persistent debates in the philosophy of biology.

Mendelian genetics is an ambiguous term, especially in the context of the philosophy of science. In most philosophical discussions, the term "Mendelian genetics" is used interchangeably with "classical genetics", or "classical Mendelian genetics". David Hull (1972, 1974, 1979), William Goosens (1978), Michael Ruse (1973, 1976) and William Wimsatt (1976) talked of "Mendelian genetics". Philip Kitcher (1984), Kenneth Schaffner (1974, 1976) and Russell Vance (1996) spoke of "classical genetics". Darden (2005) and Waters (1990) employed "classical Mendelian genetics". However, more precisely speaking, all these terms do not refer to the same thing exactly. Ruse (1973) regards Mendelian genetics as Mendel's law of segregation and of independent assortment, whereas Hull (1974) takes the chromosome theory of inheritance to be Mendelian genetics. Darden (2005) thinks that classical Mendelian genetics emerged in 1900, while Kitcher (1984) believes that classical genetics stemmed from the studies of T. H. Morgan and his fellows in 1910s.

I shall argue that all these different interpretations are just efforts to understand the same period in the history of genetics. It is evident that in the debate regarding theory reduction in genetics, all discussants well realised that the subject is the same, although there was no agreement on how to characterise it. In other words, despite the different understandings, all these terms "classical genetics", "Mendelian genetics" and "classical Mendelian genetics" refer to an early period in the history of genetics, roughly from its beginning to the introduction to the

¹⁵ Schaffner's paper "The Watson-Crick Model and Reductionism" (1969) might be the first paper on theory reduction in genetics.

molecular approach.¹⁶ For the sake of consistency, I shall call it Mendelian genetics in the rest of the thesis.

It is conventionally agreed that the history of Mendelian genetics (or genetics) started with Gregor Mendel's study of *Pisum Sativum* (pea). Gavin de Beer's following statement is a representative account of the origin of genetics¹⁷.

It is not often possible to pinpoint the origin of a whole new branch of science accurately in time and place ... But genetics is an exception, for it owes its origin to one man, Gregor Mendel, who expounded its basic principles at Brno on 8 February and 8 March 1865. (de Beer, 1965, p. 154)

In other words, Mendel, an Austrian monk in Brunn, is generally regarded as the founder of genetics. In the 1850s, Mendel began his experiments on hybridising peas. From his experiments, Mendel observed some impressive statistical regularity in the successive generations of pea hybrids. For example, when purely breeding round peas and purely breeding wrinkled ones are crossed, all of the seeds obtained in the first generation were round. More surprisingly, when these round hybrids were self-fertilised, both round and wrinkled seeds were gained in the next generation, and the ratio of round seeds to wrinkled ones was close to 3 : 1. These interesting regularities were also observed in different pairs of antagonistic traits. (See Table 1)

Table 1

The Result of the First Generation from the Hybrid Acquired by Mendel (1865)			
Experiment	Amount (of seeds with one trait)	Amount (of seeds with the other trait)	Ratio
1	5474 (round)	1850 (wrinkled)	2.96 : 1

¹⁶ It should be clarified that my usage of the term "Mendelian genetic" does not suggest that I accept that there are two genuinely distinct episodes of the history of genetics: Mendelian genetics and molecular genetics. Nor does it suggest that I accept that there is a clear-cut between these two. Since my concern is about the origin of genetics, there is no substantial difference between the expressions "the origin of Mendelian genetics" and "the origin of genetics", given that Mendelian genetics refers to an early period in the history of genetics.

¹⁷ Other similar accounts include Dodson (1955, p. 187) and Ravin (1965, p. 1).

2	6022 (yellow)	2001 (green)	3.01 : 1
3	705 (grey-brown)	224 (white)	3.15 : 1
4	882 (inflated)	299 (constricted)	2.95 : 1
5	428 (green)	152 (yellow)	2.82 : 1
6	651 (axial)	207 (terminal)	3.14 : 1
7	787 (long)	277 (short)	2.84 : 1

In addition, Mendel also observed that when two pairs of antagonistic traits are united in the hybrid by crossing, the ratio is roughly 9 : 3 : 3 : 1. For example, when the yellow and round hybrid peas are crossed, in the next generation there are 315 round and yellow peas, 101 wrinkled and yellow peas, 108 round and green peas and 32 wrinkled and green peas. These observations led to Mendel's formulation of the laws to describe and explain the phenomena.¹⁸ Mendel presented his work on *Pisum* at two meetings of the Natural History Society of Brünn in 1865 and published it entitled *Versuche über Pflanzenhybriden* shortly after.

It is traditionally (for example, Iltis, 1932; Posner & Skutil, 1968; Roberts, 1929; Stubbe, 1972; Sturtevant, 1965) said that the significance of Mendel's work on *Pisum* was not generally recognised until 1900 when Hugo de Vries, Carl Correns, and Erich von Tschermak all claimed that they independently rediscovered Mendel's work. This "rediscovery"¹⁹ marks a beginning of the examination and development of Mendel's work and its application in the science of heredity. There were many attempts to apply, develop and test the Mendelian principles on various organisms in the first decade of the twentieth century. (For example, Castle & Allen, 1903; Hurst, 1906; Nettleship, 1909; Raynor & Doncaster, 1905) However, the Mendelian principles of heredity were still controversial in the 1900s. On the one hand, there was a substantial development of the conceptualisation of the basic unit of heredity and reformulations of Mendelian laws. (For example, Bateson, 1902, 1909; R. C. Punnett, 1905) On the other hand, although the Mendelian principles were confirmed by experiments on a variety of organisms, many still refused to

¹⁸ See in-depth analysis of Mendel's work in Chapter 3 and Chapter 5.

¹⁹ I shall argue in Chapter 4 that it is not a rediscovery at all!

accept them because they were not applied universally. A breakthrough occurred in the 1910s and 1920s. By their highly sophisticated studies on *Drosophila melanogaster* (fruit fly), Thomas Hunt Morgan and his colleagues successfully integrated the Mendelian ideas in the 1900s with the chromosome theory of inheritance, in which the chromosomes were regarded as the bearers of the hereditary material. Since then, Mendelian genetics, as an established school of the study of inheritance, has been developed in a great depth and at a rapid speed.²⁰

Now, the question that interests me is: what is a best philosophical way to understand and analyse the origin of genetics? Before reviewing the traditional philosophical characterisations of the history of Mendelian genetics, I find it necessary to ward off some potential worries here. Some may question the legitimacy of my chronological demarcation of the origin of genetics: Am I justified in claiming that genetics originates from Mendel's work? I well realise that there is definitely more than one way to determine the beginning of genetics. Many historians (for example, Carlson, 2004, p. 1; Roberts, 1929, p. 286; Wallace, 1992, p. 46) maintain that the rediscovery of Mendel's work in 1900 marks the beginning of the history of genetics. Personally I am not very interested in the task of identifying the beginning of genetics with respect to an exact time. However, I have some reasons for including Mendel's research on peas in my discussion. It is a fact that Mendel's work is crucial to the history of genetics. The emergence and development of Mendelism in the first decade of the twentieth century is fundamentally based on Mendel's legacy. It is also a fact that all the debates on the Mendelian theory of heredity arose from the "rediscovery" of Mendel's work in 1900. Therefore, even if the science of genetics is "officially" established in 1900 or later, I still find it reasonable to begin my examination of the origin of genetics with Mendel's work.

In addition, I have to emphasise that my aim in this thesis is not to provide a complete and comprehensive examination of the origin of genetics. As the title of Olby's book *Origins of Mendelism* (1985) has suggested, there are multiple origins of genetics. I also recognise that there is no reason to ignore the significance of

²⁰ For a fuller account of the history of Mendelian genetics, see Carlson (2004) and Dunn (1965).

non-Mendelian elements (e.g. the development of cytology in the 19th century) in the origin of genetics. However, what I focus on here is only one path to genetics, as the subtitle of my thesis indicates. More precisely speaking, my task is to explore a best philosophical way to analyse and understand the development of scientific practice from Mendel's (1865), de Vries' (1900a, 1900c, 1900d), Correns' (1900), Tschermak's (1900a, 1900b) to Bateson's work (1902).

1.2 Traditional Philosophical Understandings of Mendelian genetics: From Laws to Patterns of Reasoning

Before the 1980s, most philosophical discussions on the history of genetics are around the debate regarding inter-theoretic reduction. In this context, it was widely discussed whether Mendelian genetics is reducible to molecular genetics. (For example, Goosens, 1978; Hull, 1972, 1979; Ruse, 1973, 1976; Schaffner, 1974; Wimsatt, 1976) In addition, a related discussion was about how to formulate the theory of Mendelian genetics. (For example, Lindenmayer & Simon, 1980; Woodger, 1937) In most of these debates, Mendelian genetics is construed as a theory without argument.

Mendelian genetics, a purely biological scientific theory is being reduced to molecular genetics, a physico-chemical theory. (Hull, 1972, p. 491)

I shall call this theory 'Mendelian genetics' in order to distinguish it from the very modern 'molecular genetics'. (Ruse, 1973, p. 12)

Immediately the question arises of what classical or Mendelian genetics includes. Both terms suggest that we are dealing with a fixed and historically dated theory. (Goosens, 1978, p. 76)

The “theory” of Mendelian genetics in most of these contexts is identified with a corpus of statements to describe and explain the phenomena of inheritance. For example, Ruse (1973, pp. 12–15) identifies the theory “Mendelian genetics” with a set of statements centred on the concept “gene”, the law of segregation, and the law of independent assortment. In other words, before the 1980s Mendelian genetics was generally understood as a single theory.

This theory-based understanding of Mendelian genetics construes Mendelian genetics as a single consistent theory universally accepted in the history. However, this implication is historically flawed. There are many significant theoretical variations in the history of Mendelian genetics, especially between 1900 and 1926. A good case is the evolution of the conception of the unit of hereditary material. In Morgan's theory of the gene (1926), the gene is a cause of morphological traits, which differentiate the varieties of organisms. For example, a pair of genes

determines the different colours of peas. There is, however, no concept “gene” found in the work of Mendel’s work (1865). Nor was it found in any early works of Mendelian genetics during the period 1900-1908. The term “gene” was coined by Wilhelm Johannsen in 1909. Nevertheless, it can be argued that there are some seemingly similar concepts (for example, “anlage”, “unit”, “allelomorph”, etc) employed in early Mendelian works in that period.

[P]rior to the definitive formation of the reproductive nuclei a complete separation of the two anlagen occurs, so that one half of the reproductive nuclei receive the anlage for [one trait], the other half the [other]. (Correns, 1966, p. 126) (Correns, 1966, p. 121)

According to the principles which I have expressed elsewhere (*Intracelluläre Pangenesis*, 1889), the specific characters of organisms are composed of separate units. (de Vries, 1966)

Each such character, ..., must henceforth be conceived of as a distinct unit-character... we may recognize this fact by naming such unit-characters *allelomorphs*. (Bateson, 1902, p. 27)

Some (for example, Sturtevant, 1965, p. 32) may argue that, despite the different names, the term “gene” and those terms quoted above are in fact the same concept, and both refer to the unit of heredity. However, these terms are clearly different concepts. Firstly, though the terms “anlage”, “unit”, “allelomorph”, and “gene” all refer to the hereditary material, their physical referents are different. Genes, for Morgan, refer to the different loci on the chromosomes in the nuclei explicitly. It was uncontroversial that “the chromosomes are the bearers of the hereditary elements or genes” (Morgan, 1926, p. 45), though the physical nature and structure of the “gene” was still unclear.²¹ However, units, for de Vries (1889), exist both inside and outside the nuclei in the cell, while Correns’ “anlage” (1900) and Bateson’s “allelomorph” (1902), both quite hypothetical, just vaguely designate

²¹ Morgan was very explicit on this point in his Nobel Prize Lecture: “Now that we locate [the genes] in the chromosomes are we justified in regarding them as material units; as chemical bodies of a higher order than molecules? Frankly, these are questions with which the working geneticists has not much concerned himself, except now and then to speculate as to the nature of postulated elements. There is not consensus of opinion amongst geneticists as to what genes are...” (Morgan, 1965, p. 315)

the hereditary material in the nuclei. Secondly, the explanation of how the gene affects the morphological trait is much more sophisticated than that of how the unit/anlage/allelomorph influences the morphological trait. In Morgan's theory (1926), genes may cause phenotypic characters in three ways: 1) One gene may cause one phenotypic character; 2) Genes at different loci in linkage groups may interact in causing one phenotypic character; 3) One gene may affect many phenotypic characters. But in the period 1900-1903, the relation of the unit/anlage/allelomorph and the morphological trait is never explicitly stated. Hence, it is not evident that the terms "gene" and the concepts "unit", "anlage", and "allelomorph" are the same concept.

Table 2

The Conceptions of the Unit of Hereditary Material		
Source	Concept	Physical Loci
Mendel (1865)	Kind of cells	Anther or Ovary
De Vries (1889, 1900a, 1900c, 1900d)	Unit	Cell
Correns (1900)	Anlage	Nuclei
Bateson (1902, 1909)	Allelomorph (or unit-character)	Nuclei
Morgan (1915; 1926)	Gene	Chromosome

Another case is the development of Mendel's laws of heredity, which were consistently regarded as a core theoretical component of Mendelian genetics between 1900 and 1926. In 1926, Morgan regards Mendel's laws as two "fundamental laws of heredity on which the modern theory of heredity was based". Mendel's two laws, namely Mendel's first law of segregation and Mendel's second law of independent assortment, are explicitly stated and articulated. (Morgan, 1926, pp. 1–10) These laws are quite different from the so-called Mendel's law(s) in the first decade of the twentieth century. Firstly, the law(s) discovered by Mendel was

named very differently: “the law of segregation” (de Vries, 1900a, 1900c, 1900d), “Mendel’s rule”²² (Correns, 1900), “the principle” (Tschermak, 1900b), “Mendel’s law” (Bateson, 1902; Davenport, 1901), “Mendel’s laws” (Weldon, 1902), etc. Secondly, all these different phrases in fact also reflect a substantial conceptual difference. Some (for example, Morgan, 1926; Weldon, 1902) carefully distinguish Mendel’s teaching into two laws, while others (for example, Correns, 1900; de Vries, 1900a, 1900c, 1900d) do not. Thirdly, the formulations of these “Mendel’s law(s)” are conceptually distinct in several substantial ways. For example, though both Weldon and Morgan identified two laws, Weldon (1902) referred them to the law of dominance and of segregation, whereas Morgan (1926) the law of segregation and of independent assortment. Moreover, even if both Weldon and Morgan have the law of segregation, they are conceptually differently. The law of segregation formulated by Weldon is about the statistical interrelations of morphological traits, while the one by Morgan is about the behaviour of genes during the process of the division of germ cells. What is more, neither Weldon’s nor Morgan’s “law of segregation” is identical with de Vries’ “law of segregation”, which is formulated in terms of antagonistic characteristics.

Table 3

Mendel’s “Law(s)” between 1900 and 1926		
Source	Name	
De Vries (1900a, 1900c, 1900d)	The law of segregation	
Correns (1900)	Mendel’s rule	
Tschermak (1900b)	The principle	
Davenport (1901)	Mendel’s law of alternative inheritance	
Weldon (1902)	Mendel’s law of alternative	The law of dominance

²² As I shall show, Piternick’s translation (1966) of the title of Correns’ paper as “G. Mendel’s Law Concerning the Behaviour of Progeny of Varietal Hybrid” is not accurate. Correns (1900) in fact used the German word *Regel*, which is better translated as rule. See more detailed discussion in Chapter 4.

	inheritance	The law of segregation
Bateson (1902, 1909)	Mendel's law	
Morgan (1915; 1926)	Mendel's first law (or the law of segregation)	
	Mendel's second law (or the law of independent assortment)	

Although, apparently, these differences do not exhaust the theoretical variations between 1900 and 1926, it is sufficient to conclude that it is extremely difficult to formulate a single theory of Mendelian genetics throughout the history, especially in the period between 1900 and 1926.

Hence, a serious problem arises for the theory-based understanding of Mendelian genetics. Given these theoretical variations, how can one identify “a theory” of Mendelian genetics? Of course it can be argued that these theoretical variations just reflect the differences between various versions of the theory of Mendelian genetics. Darden (1991) makes a detailed analysis to characterise the conceptual changes by identifying and comparing the essential theoretical components of Mendelism in 1900-1903 with those in 1926. Darden's approach is a perfect case of the theory-driven approach²³: She analyses the knowledge of Mendelian genetics by identifying the theory of the gene as a central explanatory theory. Then for the theory of gene, she analyses its central concepts and principles (or laws) in different periods (see Table 4), details how it can be applied to explain the phenomena, reconstructs how it develops and is justified, and explores the strategies for conceptual changes of the theory of the gene.

Darden's comparative analysis begins with the summary of the core theoretical components of the theory of Mendelism (1900-1903) and of the gene (1926). By carefully analysing early Mendelians' publication (Bateson, 1900, 1902; Castle, 1903; Correns, 1900; Cuénot, 1902; Davenport, 1901; de Vries, 1900a), she identifies six

²³ Coincidentally, Darden (1991, p. 7) even used the very term “theory-driven approach” to describe her approach in analysing the strategies for the theoretical changes for the theory of Mendelian genetics.

core theoretical components: unit-characters, differentiating pairs of characters, interfiled connection to cytology, dominance-recessiveness, segregation, explanation of dihybrid crosses. Based on Morgan's summary of the theory of the gene (1926, p. 25), she also identifies seven theoretical components: genes and characters, paired genes and multiple allelomorphs, interfield connection, laws of segregation, assortment, linkage and crossing-over, and mutation. By comparing these theoretical components, Darden articulates the strategy of theory change between 1900 and 1926.

Table 4

Darden's Summary (1991) of the Theoretical Changes in Mendelian genetics between 1900 and 1926		
Theoretical Knowledge	1900-1903	1926
The Unit of Inheritance	Units-Characters	Genes
	An organism is to be regarded as composed of separable units/characters. (Darden, 1991, pp. 52–54)	Genes cause characters. (Darden, 1991, pp. 169–188)
		One gene may cause one one character. (Darden, 1991, pp. 169–188)
		Multiple factors may interact in the production of one character. (Darden, 1991, pp. 169–188)
		One gene may affect many characters. (Darden, 1991, pp. 169–188)
Multiple Alleles	In varieties of organisms, the traits by which they differ are antagonistic or differentiating pairs of characters. (Darden, 1991, pp. 54–55)	In any one organism, genes occur in pairs. (Darden, 1991, p. 229)
		In a population, multiple allelomorphs for a character occasionally occur. (Darden, 1991, p. 229)

Connection with Cytology	The connections between generations are the germ cells. (Darden, 1991, pp. 55–56)	Genes are transmitted from parents to offspring in the germ cells. (Darden, 1991, pp. 229–230)
Dominance-Recessiveness	In a hybrid formed by crossing parents that differ in a single pair of characters, there is some difference such that one character dominates over the other; thus, the character in the hybrid resembles one but not the other of the parents. (Darden, 1991, pp. 56–57)	The distinction between dominance and recessiveness was deleted. (Darden, 1991, p. 72)
Mendel's Law of Segregation	In the formation of germ cells in a hybrid produced by crossing parents that differed in a single pair of characters, the parental characters segregate or separate, so that the germ cells are of one or other of the pure parental types. (Darden, 1991, pp. 57–60)	Parental genes are not modified as a result of being together in a hybrid; no new kinds of hybrid genes form. (Darden, 1991, p. 232)
	The two different types of germ cells form in approximately equal numbers. (Darden, 1991, pp. 57–60)	In the formation of germ cells of a hybrid, paired parental genes segregate so that the germ cells have one or the other of a given pair. (Darden, 1991, p. 232)
	When two hybrids are fertilised, the differing types of germ cells combine randomly. (Darden, 1991, pp. 57–60)	The two different types of germ cells are formed in equal numbers. (Darden, 1991, p. 232)
		When two similar hybrids are cross-fertilised, the differing types of germ cells combine randomly. (Darden, 1991, p. 232)

Mendel's Law of Independent Assortment	In the formation of germ cells in a hybrid produced by crossing parents that differed in two or more traits, the parental factors segregate or separate so that the germ cells are of all possible pure parental combinations. (Darden, 1991, pp. 126–132)	Genes are found in linkage groups; groups occur in corresponding pairs. (Darden, 1991, p. 149)
	The different types of germ cells are formed in equal numbers. (Darden, 1991, pp. 126–132)	Genes of different linkage group assort independently. (Darden, 1991, p. 149)
	When two hybrids are fertilised, the differing types of germ cells combine randomly. (Darden, 1991, pp. 126–132)	Usually genes in the same linkage group are inherited together; at times, however, an orderly interchange, called "crossing-over", takes place between allelomorphs in corresponding linkage groups. (Darden, 1991, pp. 149–150)
		Genes in a linkage group are arranged linearly with respect to each other. (Darden, 1991, p. 150)
		The frequency of crossing-over can be used to calculate the order and relative positions of the respective genes in linkage groups if such disturbing factors as double cross-overs and interference of one cross-over with another are taken into account. (Darden, 1991, p. 150)

Mutation	No concept "mutation". (Darden, 1991, pp. 158–160)	Genes occasionally mutate and then cause a different character. (Darden, 1991, p. 161)
		Mutation does not alter their linear relation to other genes in the linkage group. (Darden, 1991, p. 161)

Darden's detailed analysis pioneers the philosophical examination of the early theoretical development of genetics, and, in particular, makes a valuable complement to the theory-driven analysis of the history of genetics. However, such a revised theory-driven analysis is still unsatisfactory, from a historian's point of view. Darden's comparative analysis of theoretical components of the theory of Mendelism (1900-1903) and of the gene (1926) is still oversimplified. It is clear there is no such a theoretical consensus among the so-called Mendelians in the period 1900-1903 summarised by Darden. Thus, as Staffan Müller-Wille and Vitezslav Orel correctly point out, "Mendelians did not share one particular, and certainly not a particular [...] theory of inheritance." (Müller-Wille & Orel, 2007, p. 212) For example, as I have shown, there was no consensus on the formulation of Mendel's law in the 1900s. Nor was the concept "unit/character" commonly used among early Mendelians. Thus, Darden's summary fails to reflect the theoretical difference among Mendelians in the period 1900-1903.

Nevertheless, Darden's work still seems to provide a defence of the theory-driven approach in analysing the history of genetics. The difficulty of identifying the theory of Mendelian genetics is no longer a serious objection to the theory-driven approach if one argues that the theoretical variations between 1900 and 1926 well reflect the different versions of a single theory rather than different theories. Unfortunately, Darden implicitly accepts this assumption without any sustained defence. In other words, such an assumption is yet to be justified and thus, the defence is ill grounded. Even if there is one single theory with different versions, called the theory of Mendelian genetics, the problem is still not solved thoroughly. I can press the question further: What makes us convinced that these theoretical variations genuinely reflect the different versions of a single theory rather than

different theories? Even if these are different versions, what underlies the interrelation between these versions of the theory? As Kitcher points out, "[If] we think of genetic theory as something that persisted through various versions: what is the relation among the versions of classical genetic theory accepted at different times (the versions of 1910, 1930, and 1950, for example) which makes us want to count them as versions of the same theory?" (Kitcher, 1984, p. 352) If we understand Mendelian genetics as a theory, there is a difficulty of identifying *the theory* of Mendelian genetics, or the essence of the theory of Mendelian genetics. This is the first main problem of the theory-driven analysis of Mendelian genetics, namely, *the problem of theory-identification*.

In addition, despite assuming the centrality of theory in the history of genetics, the theory-driven analysis neglects an important aspect of the theory. Even if we can identify a theory of Mendelian genetics, which has been modified extensively in the history, how is this theory initially constructed and established? Once established, how is it further articulated and improved as it develops? As Darden observes, "Philosophers of science have had little to say about theory construction. Theories were treated by Popper (1965) and the logical empiricists (e.g. Hempel 1966) as if they arose all at once by a creative leap of the imagination of a scientist." (Darden, 1980, p. 151) This is the second main problem of the theory-driven analysis: *The problem of theory-construction*. As I have shown in Introduction, the problem of theory-construction is important and should be taken seriously by philosophers.

Furthermore, the theory-driven understanding of Mendelian genetics says little on the non-theoretical aspect of geneticists' practice. It is apparent that early geneticists' activities were much more than constructing theories. For example, Morgan and his colleagues took efforts to make *Drosophila*, this wild, highly variable creature, constructed into a standard instrument to be used for precise, quantitative genetic study. These non-theoretical activities are also important to the establishment and construction of the theory of the gene. Thus, the non-theoretical aspect of Mendelian genetics should not be simply ignored. This is the third main problem: *The problem of practice*.

These three problems were seldom examined before the 1980s. In order to respond

to the problem of theory-identification and of practice, Kitcher (1984) argues that Mendelian genetics is more than a single theory as a corpus of statements. Rather Mendelian genetics should be understood as a continuous series of scientific practices. The components of the practice of Mendelian genetics at a time include "a common language used to talk about heredity phenomena, a set of accepted statements in that language (the corpus of beliefs about inheritance...), a set of questions taken to be the appropriate questions to ask about hereditary phenomena, and a set of patterns of reasoning which are instantiated in answering some of the accepted questions; (also: sets of experimental procedures and methodological rules...)." (Kitcher, 1984, p. 352)

Nonetheless, Kitcher still contends that there is a theory of Mendelian genetics, and emphasises the central and essential role of this theory in the practice of Mendelian genetics. In his words, "Mendelian genetics persists as a single theory..." (Kitcher, 1984, p. 353) But, unlike the pre-1980 interpretations, he construes the theory of Mendelian genetics as a family of related patterns of reasoning for solving the "pedigree problems" (that is, identifying and explaining patterns of inheritance). A pattern of reasoning here is defined as a sequence of schematic sentences (or, a schematic argument), that is, sentences in which certain items of non-logical vocabulary have been replaced by dummy letters, together with a set of fillings instructions which specify how substitutions are to be made in the schemata to produce reasoning which instantiates the pattern. For example, the theory of Mendelian genetics in 1900 can be formulated in the following schematic argument:

- (1) There are two alleles A, a. A is dominant, a recessive.
- (2) AA and Aa individuals have trait P, aa individuals have trait P'.
- (3) The genotypes of the individuals in the pedigree are as follows: i_1 is G_1 , i_2 is G_2 , ..., i_N is G_N .
- (4) For any individual x and any alleles y, z if x has yz then the probability that x will transmit y to any one of its offspring is $1/2$.

- (5) The expected distribution of progeny genotypes in a cross between i_j and i_k is D; the expected distribution of progeny genotypes in a cross ...
- (6) The expected distribution of progeny phenotypes in a cross between i_j and i_k is E; the expected distribution of progeny phenotypes in a cross ... (Kitcher, 1989, p. 439)

Note that (1), (2), (3), and (4) are premises; (5) is obtained from (3) and (4) by using the principles of probability; (6) is derived from (2) and (5).

Similarly, the theory of Mendelian genetics in the period 1902-1910 can be formulated as follows:

- (1') There are n pertinent loci L_1, \dots, L_n . At locus L_i , there are m_i alleles a_{i1}, \dots, a_{imi} .
- (2') Individuals who are $a_{11}a_{11}a_{21}a_{21}\dots a_{n1}a_{n1}$ have trait P_1 ; individuals who are $a_{11}a_{12}a_{21}a_{21}\dots a_{n1}a_{n1}$ have trait P_2 ; . . . {Continue through all possible combinations.}
- (3') The genotypes of the individuals in the pedigree are as follows: i_1 is G_1 , i_2 is G_2 , . . . , i_n is G_n . {Appended to (3) is a demonstration that (2) and (3) are consistent with the phenotypic ascriptions given in the pedigree.}
- (4') For any individual x and for any alleles y, z , if x has yz then the probability that a particular one of x 's offspring will have y is $1/2$.
- (5') The linkage relations among the loci are given by the equations $\text{Prob}(L_i, L_j) = p_{ij}$. $\text{Prob}(L_i, L_j)$ is the probability that the alleles at L_i, L_j on the same chromosome will be transmitted together (if L_i, L_j are loci on the same chromosome pair) and is the probability that arbitrarily selected alleles at L_i, L_j will be transmitted together (otherwise). If L_i, L_j are loci on the same chromosome pair, then p_{ij} is $0.5 \leq p_{ij} \leq 1$. If L_i, L_j are on different chromosome pairs, then p_{ij} is 0.5.

(6') The expected distribution of progeny genotypes in a cross between i_j and i_k is D; the expected distribution of progeny genotypes in a cross . . .
(continued for all pairs in the pedigree for which crosses occur).

(7') The expected distribution of progeny phenotypes in a cross between i_j and i_k is E; the expected distribution of progeny phenotypes in a cross . . .
(continued for all pairs in the pedigree for which crosses occur). (Kitcher, 1989, p. 440)

In this schematic argument, (1'), (2'), (3'), (4') and (5') are premises, whereas (6') and (7') are derived from the premises.

Correspondingly, Morgan's theory of the gene in 1926 can be reformulated as follows.

(1'') There are n pertinent loci L_1, \dots, L_n . At locus L_i , there are m_i alleles a_{i1}, \dots, a_{imi} .

(2'') Individuals who are $a_{11}a_{11}a_{21}a_{21}\dots a_{n1}a_{n1}$ have trait P_1 ; individuals who are $a_{11}a_{12}a_{21}a_{21}\dots a_{n1}a_{n1}$ have trait P_2 ; . . . {Continue through all possible combinations.}

(3'') The genotypes of the individuals in the pedigree are as follows: i_1 is G_1 , i_2 is G_2 , . . . , i_n is G_n . {Appended to (3) is a demonstration that (2) and (3) are consistent with the phenotypic ascriptions given in the pedigree.}

(4'') For any individual x and for any alleles y, z , if x has vz then the probability that a particular one of x 's offspring will have y is $1/2$.

(5'') The linkage relations among the loci are given by the equations $\text{Prob}(L_i, L_j) = p_{ij}$. $\text{Prob}(L_i, L_j)$ is the probability that the alleles at L_i, L_j on the same chromosome will be transmitted together (if L_i, L_j are loci on the same chromosome pair) and is the probability that arbitrarily selected alleles at L_i, L_j will be transmitted together (otherwise). If L_i, L_j are loci on the same

chromosome pair, then $0.5 \leq P_{ij} \leq 1$. If L_i, L_j are on different chromosome pairs, then p_{ij} is 0.5.

(6'') The expected distribution of progeny genotypes in a cross between i_j and i_k is D ; the expected distribution of progeny genotypes in a cross . . .

(continued for all pairs in the pedigree for which crosses occur).

(7'') The expected distribution of progeny phenotypes in a cross between i_j and i_k is E ; the expected distribution of progeny phenotypes in a cross . . .

(continued for all pairs in the pedigree for which crosses occur). (Kitcher, 1989, pp. 440–441)

Although these three schematic arguments have different premises, they both are applied to answer the pedigree problems like: What is the expected distribution of phenotypes in a certain generation? What is the probability that a particular phenotype will result from a certain mating? ... Thus, for Kitcher, the problem of theory-identification is resolved. Despite the theoretical variations between 1900 and 1926, these seemingly different theories are in fact different versions of one theory at different times.

There are certain connections between these versions. In his words, "Mendelian genetics persists as a single theory with different versions at different times in the sense that different practices are linked by a chain of practices along which there are relatively small modifications in language, in accepted questions, and in the patterns for answering questions. In addition to this condition of historical connections, versions of classical genetic theory are bound by a common structure: each version uses certain expressions to characterise heredity phenomena, accepts as important questions of a particular form, and offers a general style of reasoning for answering those questions. Specifically, throughout the career of Mendelian genetics, the theory is directed towards answering questions about the distribution of characteristics in successive generations of a genealogy, and it proposes to answer those questions by using the probabilities of chromosome distribution to compute the probabilities of descendant genotypes." (Kitcher, 1984, pp. 353–354) In short, Mendelian genetics primarily aimed to solve "pedigree problems" (that is,

identifying and explaining patterns of inheritance); different versions of the theory of Mendelian genetics at different times contain some problem-solving patterns; and these patterns of reasoning were improved throughout the history. The changes of the premises in these schematic arguments well reflect the theoretical variations throughout the history.

Kitcher's account shows a more sophisticated understanding of the history of Mendelian genetics than those pre-1980 accounts. Firstly, it correctly suggests that the corpus of statements about the inheritance of characteristics is only one component of the practice of Mendelian genetics, and thus provides a fuller understanding of the history and practice of Mendelian genetics. Secondly, it well realises and explains away the problem of theory-identification by identifying theoretical statements about the patterns of inheritance as the premises of different but related reasoning schematic arguments. Thirdly, the problem of practice is also resolved. The experimental procedures and methodological rules are included as constituents of the practice.

Unfortunately, Kitcher's account is still problematic in several ways. Firstly, it oversimplifies the history of genetics. The theoretical variations of Mendelian genetics cannot be exhaustively characterised by the premises of Kitcher's schematic arguments. Nor do any of Kitcher's schematic arguments capture the theoretical consensus at the time suggested. Secondly, Kitcher's schematic arguments are formulated ahistorically. As I have shown, the terms like "alleles", "genotype", "phenotype" were not available in 1900. Kitcher's reformulations in terms of "alleles", "genotype" and "phenotype" fail to reflect the substantial conceptual changes from 1900 to 1920. Thirdly, Kitcher still fails to provide a sufficient description of the process of theory-construction. For instance, it is still unclear how the first version of the theory of Mendelian genetics (1900) is established. It is also unclear why there is a shift from the first to the second version of the theory of Mendelian genetics and how it happens. Although Kitcher's analysis highlights the shift of schematic arguments, the problem of theory-construction is yet to be articulated adequately. Fourthly, the problem of identification is not satisfactorily solved. Kitcher's solution to the problem of identification is to identify the pedigree problem as the underlying relation

connecting the different versions of the theory of Mendelian genetics. However, there is a “second-order” problem of identification: It is difficult to identify a version of the pedigree problem that persists throughout the history. How can Kitcher identify the problems investigated with the different versions of the pedigree problem? Finally, as I shall show in the next section, like the pre-1980 accounts, Kitcher’s understanding of Mendelian genetics is still fundamentally theory-driven in some sense.

1.3 Criticisms of the Theory-Driven Approach and Theory-Centric View

Waters (2004) challenges those traditional understandings. In the beginning of his paper "what was Mendelian genetics?", he compares the traditional philosophical accounts with a recent historical account by Robert Kohler (1994). According to this account, Mendelian genetics is organised around the efforts to investigate a broad range of basic biological phenomena, not just transmission phenomena. Moreover, Kohler provides an account of the central research agendas of Mendelian genetics without mentioning the central theory that explained inheritance patterns. Although, as Waters realises, it does not necessarily show that the theory was irrelevant to Mendelian genetics, it does suggest that the research of Mendelian genetics was not merely organised around efforts to improve theoretical explanations of gene transmission and expand upon the range of inheritance phenomena explicable in terms of the theory. A theory-based picture of the history of Mendelian genetics is not a complete presentation of the history of Mendelian genetics.

Hence, Waters believe that there is a puzzle for philosophers. On the one hand, the research of Mendelian genetics entailed many theoretical explanations of inheritance patterns. On the other hand, many research agendas of Mendelian genetics can be described without mentioning these theoretical explanations.

Waters's solution to this puzzle is to criticise the traditional account for mistaking the *means* for the *ends*: "[E]xplanations of inheritance patterns are an essential part of the *means* for advancing the research agendas of classical genetics, but that research agendas are not ultimately aimed at explaining inheritance patterns." (Waters, 2004, p. 786) For Waters, explaining inheritance patterns does not exhaust practices of classical geneticists. He shows this by scrutinising Alfred Sturtevant's investigation of a crossover modifier $C_{III B}$ (1926).

In the 1910s, Morgan and his collaborators proposed the theory of the gene, which states that the morphological traits of an individual are referable to paired genes in the chromosomes that are held together in a definite number of linkage groups. Each pair of genes separates when the germ cells mature and recombines with the pair of genes from the other parent to form a new pair of genes. However, the

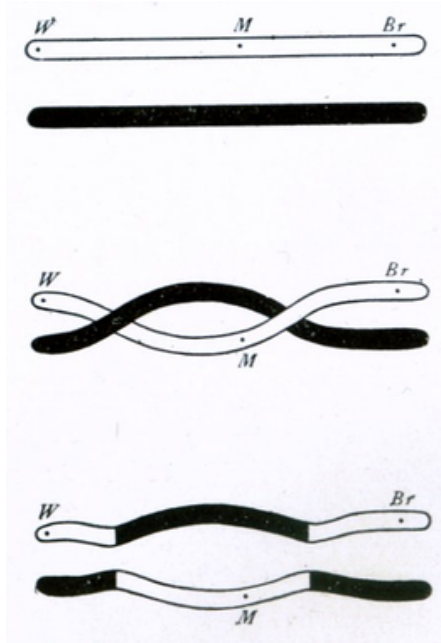


Figure 1 Crossing Over

paired genes may not always be linked completely. The genes in one chromosome may be interchanged for the genes in the other chromosome. (See Figure 1 Crossing Over) This phenomenon of interchange is called crossing over.

In the 1920s, it was observed that the frequency of crossing over between any two loci varies with temperature, age of parents, chromosomal context of the segment containing the loci, and the presence of crossover modifiers on the same chromosome. The first crossover modifier found in *Drosophila*, $C_{III A}$ ²⁴, reduced the frequency of crossing over in the region around ebony in the third chromosome. This modifier did not reduce the frequency of crossing over when present in homozygous form. Shortly thereafter some other crossover modifiers were discovered. At first, it was thought that the crossover modifiers were mutant genes and geneticists mapped their locations in the chromosome. However, Sturtevant pointed out that the cause of the decrease in the frequency of crossing over is an inverted section of the chromosome rather than a mutation of a single gene. (See Figure 2 (Sturtevant, 1926, p. 699)²⁵) He mapped the region around $C_{III B}$ and showed that the order the genes in the affected region was reversed. According to

²⁴ C designates a crossover modifier, and the capitalization means that it is a dominant. The Roman III designates its locus as in the third-chromosome.

²⁵ I acknowledge the permission to reprint this figure from Elsevier.

Sturtevant, the frequency of crossing over was reduced in the third chromosome where $C_{III B}$ was present in heterozygous form because genes in the inverted region around $C_{III B}$ were not positioned across from the corresponding genes in the wild type chromosome during meiosis. On the other hand, the frequency of crossing over was not reduced in flies homozygous for $C_{III B}$ because the order of the genes was the same in the two third-chromosomes of these flies.

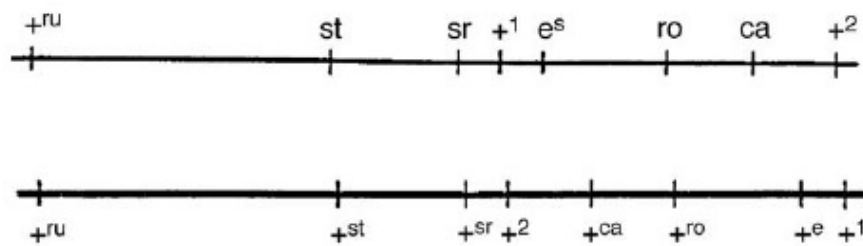


Figure 2 (Sturtevant, 1926, p. 699)

In addition to explaining the patterns of inheritance, Sturtevant's investigation of the $C_{III B}$ also explains the synaptic attraction between chromosomes during the process of meiosis. As Waters neatly summarises, "Sturtevant's finding that chromosomal inversions reduced crossover was important because it favoured the idea the mutual attraction between genes was responsible for the mutual attraction between homologous chromosomes during meiosis and because it suggested that the process of crossing over depended on the close affinity homologous genes." (Waters, 2004, pp. 791–792) In other words, the investigation of the crossover modifier is not only to explain some patterns of inheritance, but also to reveal some information about basic biological processes (i.e. meiosis). Moreover, Waters emphasises that Sturtevant's research on the crossover modifier illustrated was central to the practice of Mendelian genetics in the later 1920s, 1930s and 1940s.

Therefore, Waters counters the unexamined assumption behind the traditional theory-driven approach in analysing the history of Mendelian genetics: The history of Mendelian genetics was centred on the development of a theory of gene transmission, and the practice of Mendelian genetics is organised around efforts to improve the theory's explanations of heredity and to expand the range of

inheritance phenomena that it could explain.

As Waters has shown in the Sturtevant's case, the practice of Mendelian genetics was not ultimately theory-driven. There are many investigative practices (e.g. Sturtevant's study of $C_{III B}$) in Mendelian genetics without such purposes. These investigative practices should not be overlooked in analysing the history of Mendelian genetics. As Waters pointed out, "[T]he methods associated with genetic analysis and the genetic approach to studying biological processes were as integral a part of classical genetics as were the principles of independent assortment and segregation." (Waters, 2004, p. 800) In other words, Waters suggests that philosophers should not simply take a monistic understanding of the aim of Mendelian genetics. Focusing on explanations of inheritance only provides a superficial understanding of the history of Mendelian genetics. Not all practices of Mendelian genetics were centred on a central explanatory theory. Thus, Waters contends that taking the theory-driven approach to analysing the history of Mendelian genetics relies on a problematic assumption that the practice of Mendelian genetics is centred on an explanatory theory. (*The Problem of Theory-Centrality*)

Thus, given the problem of theory-centrality, Waters argues that the pre-1980 traditional accounts are inadequate for understanding the actual practice of Mendelian genetics. Furthermore, Waters's criticism is also applied to Kitcher's account of Mendelian genetics in terms of practices. Although Kitcher realised that experimental procedures and methodological rules are components of the practice of Mendelian genetics, he still contended that these practical elements are designed for use in evaluating the theoretical consequences. He explicitly claimed that "these [practical elements] may be ignored for [the purpose of understanding the state of a science at a time]." (Kitcher, 1984, p. 352) In other words, Kitcher's account of Mendelian genetics is still theory-driven.

Along with Waters, I contend that that the theory-driven understanding of Mendelian genetics is inadequate. Moreover, based on Waters' objection on theory-driven approach, I wish to articulate the problems of the traditional theory-driven analyses of Mendelian genetics more explicitly. The theory-driven

approach is deeply rooted in an unexamined assumption, that is, the history of Mendelian genetics should be characterised and structured by a central explanatory theory. This assumption well reflects a view widely accepted by philosophers that there is a theory *T*, which is essential and central to the practice of Mendelian genetics in the sense that the practice of Mendelian genetics is ultimately driven by *T*. To say that the practice of Mendelian genetics is ultimately driven by *T* not only means that *T* is accepted for all the practices of Mendelian genetics, but also that the practice of Mendelian genetics is organised around the efforts to apply, articulate, extend and improve *T*. This is what I call the theory-centric view.

Note that this theory-centric view (or, theory-centrism) is more than an unexamined assumption of the philosophical examination of the history of Mendelian genetics. It also reflects a widespread philosophical assumption that scientific practice is ultimately is organised around efforts to fill out a theory, and thus a school of scientific practice or an episode of the history of a science should be characterised and structured by a theory.

Three further points have to be clarified. Firstly, the theory-centric view is not a view about the nature of the theory, but about the role of the theory in (the history and practice of) science. The theory-centric view of science only makes a commitment to the importance of theory in science, whether a theory is construed in terms of statements, models, or patterns of reasoning. The question regarding the nature of theory given the acceptance of the theory-centric view of science still remains. For example, though Kitcher (1984, 1989) and Balzer (1986; 2000) clearly disagree on what a theory is, both of their characterisations of Mendelian genetics are theory-driven.

Secondly, the theory-centric view of science is not just the view that theories are indispensable for scientific practice. In fact the theory-centric view of science is stronger than the claim that theories are indispensable for scientific practice. The theory-centric view of science entails that theories are indispensable for scientific practice, but not *vice versa*. It should be noted that when I say that theories are indispensable for scientific practice, it only means that for any scientific practice *P*,

there must be some theories that play an important role. It does not warrant or imply that there must be some theories, which are essential and central to *P*.

Thirdly, the theory-centric view is different from the theory-driven approach. The theory-driven approach is an approach adopted by philosophers to analysing the history and practice of science, while the theory-centric view is an assumption underlying and justifying the theory-driven approach.

Unfortunately, this theory-centric view is highly problematic, especially in the case of Mendelian genetics. Firstly, given the significance of a central explanatory theory in the practice of genetics, it seems necessary to identify what that theory is. However, as I have shown in the section 1.2, it is extremely difficulty to identify such a theory. Thus, it is doubtful that there is a central explanatory theory as the driving force of the practice of genetics. This is the source of the problem of theory-identification.

Secondly, when analysing the history of Mendelian genetics, the philosophers with the theory-centric view in mind keeps asking perplexing questions as follows:

- (1) What is the theory of Mendelian genetics? (For example, Goosens, 1978; Kitcher, 1984; Ruse, 1973)
- (2) How should the theory of Mendelian genetics be formulated? (For example, Balzer and Dawe 1986; Balzer and Lorenzano 2000; Lindenmayer and Simon 1980; Woodger 1937)
- (3) What is the relation between the theory of Mendelian genetics and that of molecular genetics? (For example, Hull, 1972; Kitcher, 1984; Schaffner, 1969; Waters, 1990)
- (4) What is a “gene”? (For example, Beurton, Falk, & Rheinberger, 2000; Malisoff, 1939)

It should be noted that these questions are not bad questions themselves. However, the theory-centric view pushes one to look for a unitary answer to questions like (1), (2) and (4). Since the theory-centric account of Mendelian genetics emphasises the

essentiality and centrality of a theory, it seems implausible that such a theory might be understood pluralistically. Even if as Kitcher admits that the theory of Mendelian genetics is a theory with different versions, he still has to show that there is something common and unchanged underlying these versions. Thereafter, a further unitary answer is required to the question that what makes the different theoretical knowledge to be different versions of one single theory. Unfortunately, as I have shown in the section 1.2, it is extremely difficult to formulate the so-called theory of Mendelian genetics, so it is likely that there is no such a monist account of the theory of Mendelian genetics at all. If so, questions like (3) are no longer philosophically significant, since the problem of theory reduction relies on the assumption that there are two unitarily formulated theories. Hence, questions like (1), (2), (3) and (4) are misleading.

Thirdly, the theory-centric view pushes philosophers to hold an oversimplified understanding of the development of Mendelian genetics. A consequence of the theory-centric Mendelian genetics is that the practice of Mendelian genetics aims to look for a theory with a great explanatory power. It is definitely misleading and ahistorical. It is a fact that neither Mendel's study on *Pisum*²⁶ or Morgan's study on *Drosophila* initially aimed to look for a theory to explain the phenomena of inheritance. It is also evident, as Waters shows, that there are many significant contributions (e.g. investigation of a crossover modifier $C_{III B}$) by classical geneticists, which are not aimed at applying, extending or improving the theory of Mendelian genetics.

Now I conclude that the theory-driven analyses of the history of genetics are problematic in the sense that both the theory-driven approach and its underlying assumption are problematic. Thus, it seems to be a good time to explore a new approach to analysing and interpreting the history of genetics, especially the origin of genetics.

Summary

In this Chapter, I have briefly introduced the history of Mendelian genetics and shown that most of the traditional philosophical analyses of it are theory-driven. In

²⁶ For more discussion, see Chapter 3.

addition, I have also articulated the four main problems of the theory-driven analyses: The problem of theory-identification, the problem of theory-construction, the problem of practice, and the problem of theory-centrality. Moreover, I have articulated and critically examined the assumption underlying the theory-driven approach.

2

An Introduction to the Exemplar-Based Approach

Despite its dominance in the twentieth century's philosophy of science, the theory-driven approach was not without enemies. Thomas Kuhn, in his book *The Structure of Scientific Revolutions* (1962), strongly opposes the unexamined assumption among philosophers that the theory should be the unit of analysis in the philosophical examination of history of science. In particular, Kuhn (1970b, p. 182) argues that the received understanding of theory “connotes a structure far more limited in nature and scope” to reflect the multifaceted practice of a community of scientists. In this chapter, I shall critically review and articulate Kuhn’s paradigm-based methodology. Then, inspired by Kuhn’s notion of “exemplar”, I shall propose a new definition of exemplar, and outline an exemplar-based approach as an alternative to the theory-driven one to analysing the history of scientific practice.

2.1 The Kuhnian Analyses of Mendel’s Contribution

For Kuhn, the typical unit of analysis should be a paradigm rather than a theory. Accordingly, Kuhn suggests that the history of a science is a cyclic process alternating the period of normal science, in which most scientists work under one dominating paradigm, with the period of scientific revolution, in which there are

multiple competing paradigms. In the period of normal science, scientists' main task is to solve puzzles or problems of the accepted paradigm. Sometimes a paradigm falls into a state of crisis due to some internal and external factors when the scientists begin to lose their confidence in the ability and effectiveness of the paradigm's puzzle-solving machinery. For Kuhn, a crisis is "the usual prelude" to a scientific revolution, or paradigm-shift. In the period of scientific revolution, there is no universally accepted paradigm in the community of scientists. Multiple paradigms compete with each other until the establishment of a new period of normal science (i.e. one of the competing paradigms wins the support of the majority and most scientists again work together to solve its puzzles).

This Kuhnian account of the history of science provides an alternative way to analyse the history of science, including the history of genetics. On the basis of his reinterpretation of Mendel's work, Augustine Brannigan (1979) adopts Kuhn's conceptual framework to reassess Mendel's contribution:

[I]n 1866 Mendel's work figured as normal science in the hybridist tradition, while in 1900 the revival of Mendel's discovery of segregation constituted a relatively revolutionary achievement. (Brannigan, 1979, p. 424)

According to Brannigan, Mendel's work on *Pisum* plays a dual role in the history of science. On the one hand, it is well within the paradigm of hybridism²⁷. The main problem that Mendel aimed to solve is "the role of hybridization in the evolutionary history of organic forms", which was an unsolved puzzle left by early hybridists. On the other hand, Mendel's work was adopted by the rediscoverers to constitute a scientific revolution in the history of the science of heredity. Thus, from his contemporaries' point of view, Mendel's work was part of the paradigm of hybridism, while from the rediscoverers' point of view, some of Mendel's work played a key role in the a revolution in the science of heredity in 1900.

Müller-Wille and Orel (2007) recently provide a similar Kuhnian interpretation.

Mendel's achievement was a product of normal science, and yet a revolutionary step forward. (Müller-Wille & Orel, 2007, p. 171)

²⁷ For a brief history of hybridism, see the section 3.1.

Along with Brannigan, Müller-Wille and Orel argue that Mendel's work was an extension of early hybridists' (especially Gärtner's) work. They convincingly show that there is a continuity of works by Linnaeus, Kölreuter, and Gärtner, linked with anomalies and puzzles under an accepted paradigm. However, there is one substantial difference between Brannigan's and Müller-Wille's and Orel's interpretations. Müller-Wille and Orel contend that Mendel's work itself was revolutionary.

As we shall see in Chapter 3 and 4, from a historical point of view, both interpretations are more sophisticated than the theory-based ones discussed in Chapter 1. Unlike the theory-driven analyses, Mendel's theory is not simply construed as a theory of heredity without argument. Mendel's work is examined in its historical context. For example, the hybridist influence on Mendel is well characterised and highlighted in these Kuhnian interpretations. However, the role of Mendel's work in 1900 has yet been articulated adequately. Brannigan is unclear on how and to what extent Mendel's work was adopted and constituted the Mendelian revolution in 1900, while Müller-Wille's and Orel's philosophical interpretation that Mendel's work was revolutionary is based on their controversial²⁸ historical argument that Mendel's work can be understood as a work of heredity.

Nevertheless, these Kuhnian analyses suggest a promising way to analyse and characterise the origin of genetics from Mendel to Bateson. In order to explore a more sophisticated paradigm-based approach, I shall first review Kuhn's conception of paradigm in detail.

²⁸ For in-depth discussions, see the section 3.3.

2.2 Revisiting Kuhn's Paradigm

Kuhn (1962) proposes that the practice of a scientific community should be better analysed and characterised in terms of paradigms than of theories. Kuhn's proposal can be understood in two ways, given his elaboration of two senses of paradigm (Kuhn, 1970b, 1974): paradigm-as-disciplinary matrix and paradigm-as-exemplar. One interpretation of Kuhn's proposal is that a paradigm (-as-disciplinary matrix) should be a better candidate to represent and reflect the practice of a scientific community than a theory. The disciplinary matrix (the broad sense of "paradigm") is defined as a consensus around a variety of components of activities shared by the members of a given scientific community.²⁹ Kuhn's favourite examples of disciplinary matrices include Aristotelian physics, Ptolemaic astronomy and Newtonian mechanics. (Kuhn, 1970b, p. 10)

There are four main constituents of a disciplinary matrix: symbolic generalisation, model, value, and exemplar (the narrow sense of "paradigm"). Symbolic generalisations are symbolic expressions of scientific hypotheses, which can be manipulated mathematically. Models, for Kuhn, designate two different classes. On the one hand, models include "the metaphysical commitments" or "ontological models"³⁰ like the belief that the heat of a body is the kinetic energy of its constituent particles. On the other hand, models also encompass the "heuristic models and analogies" in accordance with which phenomena from a given class

²⁹ Kuhn defines a disciplinary matrix as what the members of a scientific community share. This definition emphasises the importance of scientific communities in the understanding of the history of science. Scientific communities can be isolated without prior recourse to theoretical agreements, while disciplinary matrices have to be determined by scrutinising the behaviours and practice of a given community's members. This definition highlights Kuhn's belief that all scientific practices are community-based activities. As Kuhn put it, "[a] paradigm governs, in the first instance, not a subject matter but rather a group of practitioners. Any study of paradigm-directed or of paradigm-shattering research must begin by locating the responsible group or groups." (Kuhn, 1970b, p. 180) Here Kuhn, unlike his most contemporaries (perhaps I shall say philosophers), took a very different perspective of the history of science. From his point of view, the subject is not theories but what the community of scientists share. As to how to isolate a scientific community without prior recourse to theoretical agreements, Kuhn provides a rough methodology by examining attendance at special conferences, the distribution of draft manuscripts prior to publication, and all formal and informal communication networks including those in correspondence and in the lineages of citations. And he also assumes that a "more systematic means" for the identification of a scientific community will be forthcoming. (Kuhn, 1970b, pp. 177–178, 1974, pp. 461–462)

³⁰ Kuhn did not explicitly define the so called "metaphysical commitments" in addition to giving two examples. As to the heat example, it seems more proper to call it the definition of heat than the metaphysical commitment of heat.

may be treated as if they were something else entirely. Take an example from Mendelian genetics: Genes carried on chromosomes can be understood as beads strung on a wire.³¹ The values of a disciplinary matrix, which are shared by the members under it (Kuhn, 1970b, p. 185, 1977a, pp. 321–322)³², include accuracy³³, consistency³⁴, scope³⁵, simplicity³⁶, fruitfulness³⁷ and so on³⁸. The exemplar, which Kuhn claimed "the most novel and least understood aspect of [SSR]", is originally defined as "a set of recurrent and quasi-standard illustrations of various theories in their conceptual, observational and instrumental applications. These are the community's paradigms, revealed in its textbooks, lectures and laboratory exercises." (Kuhn, 1970b, p. 43) According to a later definition (Kuhn, 1974), the exemplars are the "concrete problem-solutions"³⁹. Thus, accordingly, a paradigm (-as-disciplinary matrix) shift involves the change of symbolic generalisations, models, values, and exemplars.

Traditionally, most philosophers including Kuhn himself used to take disciplinary matrix as an alternative to theory to analyse the history of science, since a

³¹ It is not difficult to see that Kuhn's definition of "model" is not well developed. For example, the nature of model is not discussed. Scientific model has been becoming one of the central topics in the philosophy of science since 1970s, but unfortunately Kuhn did not further articulate a refined account of "models" in his later academic career.

³² Kuhn (1977a) uses "theory" and "paradigm" interchangeably. For the sake of consistency, I re-formulate these values in terms of disciplinary matrix.

³³ A disciplinary matrix should be both qualitatively and quantitatively accurate, that is, the consequences (or predictions) of the disciplinary matrix should be in demonstrated agreement with the results of existing observations and experiments. And to what extent the qualitative and quantitative accuracy is enough is shared by the members under that disciplinary matrix.

³⁴ The components of a disciplinary matrix should be consistent and compatible with other well-established disciplinary matrices. The members of the scientific community share a commitment to the standard of consistency.

³⁵ A disciplinary matrix should have a broad scope in the sense that the consequences of a disciplinary matrix should extend far beyond the particular observations it was initially designed to account for.

³⁶ A disciplinary matrix should provide unifying explanations for the ordering of unrelated groups of phenomena and have the simplest conceptual and technical apparatus and procedures for application. The standard of simplicity is universally accepted within the scientific community.

³⁷ A disciplinary matrix should disclose new phenomena or new relations between previously known phenomena.

³⁸ In addition, Kuhn (1970a) occasionally regards the unity of science, explanatory power and plausibility as values of a disciplinary matrix.

³⁹ Kuhn does not explicitly define what a "concrete" problem means. By the examples he gives, the concrete problems seem to be the problems in the actual practice. But are there any problems not problems in the actual practice? Thus, the predicate "concrete" seems unnecessary and redundant, and I shall use the term "problem-solution" instead in the following.

disciplinary matrix encompasses a more dimensions of the practice of a scientific community than a theory does. For example, Kuhn (1970b, pp. 55–56, 107) contends that the chemical revolution is better characterised as a shift between two disciplinary matrices rather than one between two theories. This plan looks appealing, but the disciplinary matrix-based approach encounters a similar problem that threatens the theory-driven approach: *the problem of paradigm-identification*. When looking at a historical case, it is very difficult to identify a set of symbolic generalisations, models, values, and exemplars, which is invariantly and universally accepted by the community throughout the period of normal science. In addition, the constituents of a disciplinary matrix, especially models and exemplars, are insufficiently articulated in Kuhn’s work.

The other way to understand Kuhn’s proposal that the practice of a scientific community should be better analysed and characterised in terms of paradigms rather than theories is that an exemplar is a better candidate to characterise the most fundamental unit shared by a scientific community than a theory is.

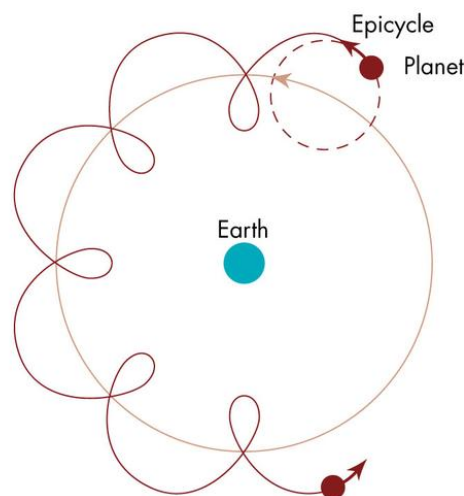


Figure 3

An exemplar, as I mentioned, is defined by Kuhn as a concrete problem-solution. Ptolemy’s solution by applying epicycles to the problem of accounting for the retrograde motion of Saturn is a good example of an exemplar. Ptolemy used a geometric model to explain the variations in speed and orbit of the motion of

Saturn.⁴⁰ In the simplest form, Saturn moves on a small circle (an epicycle), whose centre moves on the large circle (a deferent). (See Figure 3) At his time, Ptolemy's application of epicycles was a great scientific achievement as a tool to describe and predict the motion of Saturn.

For Kuhn, exemplars are more than concrete problem-solutions. The example of Ptolemy's application of epicycle highlights four normative functions of exemplar⁴¹. Firstly, exemplars have a semantic function. Some concepts are not only employed in exemplars, but also acquire their meanings with the articulation of exemplars. In the above example, the concept "epicycle" can be better understood by an exemplary application of it. And it is not an isolated case. As Kuhn puts it, "Without exemplars [one] would never learn much of what the group knows about such fundamental concepts as force and field, element and compound, or nucleus and cell." (Kuhn, 1974, p. 471)

Secondly, exemplars have an investigative function by suggesting new puzzles for the paradigm. (Kuhn, 1970b, p. x) For example, applying one epicycle to the circular orbit of Saturn is a great improvement in explaining the retrograde motion of Saturn, but it does not perfectly fit the actual observation of the motion of Saturn. Hence a new puzzle occurs: How can it be resolved? Of course, this is just one kind of puzzle suggested by exemplars. There are many other kinds. In some cases, the symbolic generalisations employed by an exemplar may involve a constant whose value is not known with precision (e.g. the articulation of the gravitational constant in the law of gravitation); an exemplar may employ approximations that could be improved; it may suggest other puzzles of the same kind (e.g. whether a similar solution can be applied to a similar problem); it may suggest new areas for investigation (e.g. what is the physical referent for a concept used in an exemplar).

Thirdly, exemplars have an explanatory function by providing approaches to other problems. (Kuhn, 1970b, p. x) The application of epicycle in formulating Saturn's orbit to account for its retrograde motion indicates a similar and potential solution

⁴⁰ Ptolemy was not the first to develop this model. It is believed that the application of epicycle can be traced back to Apollonius of Perga and Hipparchus of Rhodes.

⁴¹ Hoyningen-Huene (1993) summarised three functions for exemplars, and Bird (2000) identified four. My interpretation of the functions of exemplars is slightly different from theirs.

to the puzzle of describing Saturn's retrograde motion.

Fourthly, exemplars have an evaluative function by providing standards to assess potential problem-solutions. (Kuhn, 1970b, p. 103) The concepts, models, and values employed in different exemplars in a disciplinary matrix have to be consistent. And the solutions to the similar problems are assessed with respect to the similarity of the exemplary solution. For example, the explanation of the retrograde motion of Mercury by applying epicycles is acceptable for Ptolemaic astronomers since it is consistent and similar to Ptolemy's solution by applying epicycles to the problem of accounting for the retrograde motion of Saturn. In contrast, Priestley, as a practitioner of the phlogiston paradigm (as a disciplinary matrix) of combustion, refused to accept Lavoisier's solution by employing the concept "oxygen" to the problem of accounting for combustion, since it contradicted the fundamental exemplar of the phlogiston paradigm (as a disciplinary matrix). Moreover, exemplars contribute to establish standards as well as other sorts of components of a disciplinary matrix. As Paul Hoyningen-Huene summarises, "For a judgement regarding the acceptability of a proposed problem solution is an evaluation of this proposal undertaken relative to accepted symbolic generalizations, ontological commitments, the heuristic models current in the community, and accepted standards of accuracy, simplicity, and the like." (Hoyningen-Huene, 1993, p. 162)

The normative functions highlight the significance of exemplar in the scientific practice. Moreover, Kuhn has three reasons⁴² for his preference of exemplars.

Firstly, when investigating the history and practice of a particular scientific community, it is much easier to find shared exemplars than to find shared theories as a guide to the practice of this scientific community. (Kuhn, 1970b, pp. 43–44) The scientists of a particular community can agree that an exemplar provides a solution to a research problem but disagree about some of the concepts, laws and theories postulated by that exemplar. For example, Stahl, Priestley and Cavendish accept the explanation of the phenomenon of combustion by appeal to the phlogiston model,

⁴² In fact, Kuhn (1970b) identified four reasons for the priority of exemplars. But the fourth reason is implausible, and he later (1974, p. 471 n.17) also admitted this, so I decide not to state it here.

but they differ in the identification of the properties of phlogiston. As a result, the search for a set of shared theories, the so-called theory of phlogiston, between Stahl, Priestley and Cavendish is more difficult and less satisfying than the search for a shared exemplar. As Hoyningen-Huene remarks, "The coherence of the research tradition associated with [a core of common, concrete problem solutions] is a consequence of the fact that scientists find and process their research problems by forming analogies to these exemplary problem solutions... the attempt to reconstruct a set of rules assumed to underlie research practice implicitly generally misses its mark." (Hoyningen-Huene, 1993, p. 137)

Secondly, scientists cannot learn concepts, laws and theories without exemplars. (Kuhn, 1970b, pp. 46–47) In Kuhn's words, "Scientists... never learn concepts, laws and theories in the abstract and by themselves... A new theory is always announced together with applications to some concrete range of natural phenomena; without them it would not be even a candidate for acceptance." (Kuhn, 1970b, p. 46) In the example of Ptolemy's solution to the problem of retrograde motion, the concept "epicycle" is articulated by the exemplar. It is evident that concepts, laws and theories are directly learned through repeated exposure of exemplars, not vice versa. As Kuhn emphasises, "[i]n absence of ... exemplars, the laws and theories [a student] has previously learned would have little empirical content." (Kuhn, 1970b, p. 188) In this sense, exemplars play a more fundamental role than theories do in the scientific practice.

Thirdly, the history of science shows that the practice of a scientific community can develop without shared theories as long as there are shared exemplars. (Kuhn, 1970b, pp. 47–48) Consider the history of the phlogiston theory⁴³. Despite the disagreement on the properties of phlogiston, there is a continuous series of practices of a community including Priestley and Cavendish who worked on the basis of the exemplary solution to the problem of accounting for combustion in terms of phlogiston. Therefore, Kuhn argues that the exemplar is a better candidate to reflect and represent the practice and history of science.

⁴³ When I say "the history of the phlogiston theory", I do not mean a history of a theory, namely the phlogiston theory. Rather I mean a school of scientific practice in the 18th century. The reason I call it "the phlogiston theory" is just to follow the convention.

To sum up, there are two ways of understanding Kuhn's proposal that a scientific achievement should be better understood in terms of paradigms than of theories. In the broad sense, a paradigm-as-disciplinary matrix should be a better candidate to represent and reflect a school of scientific practice in the history of science. In the narrow sense, a paradigm-as-exemplar should be a better candidate to characterise the fundamental unit shared by a scientific community. Correspondingly, we can learn two paradigm-based approaches from Kuhn. According to the disciplinary matrix-based approach, when analysing the history of science, one should first identify a disciplinary matrix by articulating the shared symbolic generalisations, models, values, and exemplars. Then one should further analyse these constituents of the disciplinary matrix, detail how they can be applied to solve puzzles, reconstruct how they develop and explore the development of the disciplinary matrix as a puzzle-solving machinery. However, given the inadequate explication of "model", "value", and "exemplar" and their significance to the determination of a disciplinary matrix, there is too much work to be done to explore and defend the disciplinary matrix-based approach. Thus, this is not the approach I aim to explore and defend in this thesis. Rather, I shall focus on the notion of exemplar and its application as a tool to analyse the history of science. Before delving into my articulation of exemplar, I shall carefully re-examine Kuhn's characterisation of exemplar.

Prospects of an Exemplar-based Approach

Exemplar is a key concept in Kuhn's early philosophy of science (1962, 1970b, 1974). Puzzle-solving is the most common and characteristic activity in the period of normal science, and even symbolises the scientific character to some extent⁴⁴. As I have reviewed, exemplars as problem-solutions play an indispensable role in the practice of puzzle-solving. It is Kuhn's novel contribution to the significance of puzzle-solving in the scientific practice into the philosophy of science community. However, Kuhn's conception of "exemplar" still lacks of a full articulation. Nor has a Kuhnian exemplar-based approach ever been explored seriously to analyse the

⁴⁴ Kuhn (1970a) once argues that it is puzzle-solvability rather than falsifiability that is the criterion of scientific character.

history or practice of science.⁴⁵ One reason might be that Kuhn no longer continued to develop his account of the history of science in terms of exemplars, neither by presenting a detailed historical case-study, nor providing a more sophisticated conceptual analysis of the notion of exemplar. In particular, Kuhn's own definition of exemplar is too thin and premature. Many significant problems concerning exemplars are yet to be explored. Firstly, Kuhn says little on how an exemplar is first established or constructed further. Although he is famous for his rejection of the sharp distinction between the context of discovery and of justification and accusing philosophers of ignoring the "temporal development of a theory", Kuhn does not provide a sophisticated account of the construction and temporal development of an exemplar. Secondly, in his elaboration, Kuhn's "exemplar" is simply exemplified by the examples in the textbooks, lectures, and laboratory exercises. The constituents of an exemplar are never explicitly explicated. Nor is a historical example of an exemplar articulated in an explicit way. Thirdly, Kuhn's "exemplar" (as a problem-solution) implicitly assumes some pre-existing problems. But where are these pre-existing problems from? Although contending that the shift of accepted exemplars in a scientific revolution necessitates the redefinition of research problems (Kuhn, 1970b, p. 103), he says little on how the research problems are defined. Nor is clear if problem-defining is a task for the construction of an exemplar. The significance of problem-defining seems to be neglected by Kuhn. Fourthly, Kuhn fails to explore the characteristics of a good exemplar. It is unclear what makes some exemplars successfully accepted, while others neglected or abandoned.⁴⁶

Therefore, it seems clear that a promising exemplar-based approach has to rely on a more sophisticated articulation of exemplar and overcome all the problems of Kuhn's conception of exemplar. In the next section, I shall articulate and explore a new interpretation of exemplar and thereof an outline of the exemplar-based

⁴⁵ There are a few attempts to employ the notion of exemplar to analyse some history cases. For example, Darden (1991) analyses the explanatory virtue of the hybrid crossing in terms of exemplar, while Skopek (2011) explores the pedagogical virtue of Mendel's work on peas in terms of exemplar. Unfortunately, the exemplar, for both Darden and Skopek, is simply construed as the example in the textbook.

⁴⁶ As I have mentioned, Kuhn listed five main characteristics of a good theory (or a paradigm). (Kuhn, 1977a, pp. 321–322) However the theory (or the paradigm) here refers obviously to a disciplinary matrix rather than an exemplar.

approach.

2.3 The New Definition of Exemplar and the Exemplar-based Approach

As I have argued in the last section, Kuhn's definition of exemplar is not well articulated mainly in four ways:

- 1) The constituents of an exemplar are unclear;
- 2) The construction of an exemplar is unclear;
- 3) No detailed example of an exemplar is given.
- 4) What makes an exemplar successfully received is unclear.

Correspondingly, a good reinterpretation of exemplar has to

- 1') analyse the constituents of an exemplar;
- 2') explicate how an exemplar is constructed;
- 3') be instantiated by a detailed historical case-study.
- 4') explore the characteristics of a successfully accepted exemplar

In other words, I not only have to tell what an exemplar is, what the components of an exemplar are, but also to explore how an exemplar is constructed, how an episode of the history of science is best characterised in terms of exemplars by my case study of the origin of Mendelian genetics. Moreover, I shall discuss what the characteristics of a good exemplar are, which make it successfully accepted.

I have argued that one advantage of a Kuhnian exemplar-based account of the history of science is that the significance of the problem-solution in the history and practice of science is well articulated and highlighted. Many of scientific practices in history are oriented or inspired by some past successful problem-solutions. Kuhn's account of "puzzle-solving" does capture the "essence" of many, though not all, scientific practices in history. Therefore, I would reserve this fundamental part of Kuhn's idea that a key constituent of an exemplar is a problem-solution. Furthermore, I argue that an exemplar as the fundamental unit shared by a scientific community should be more than a problem-solution. A well-defined

problem itself is at least as important as its solution in the scientific practice. It also has as many normative functions as its solution does. In many historical cases, puzzle-solving and problem-defining are two intertwined activities. As I shall show in Chapter 5, an exemplary practice involves the mutually related activities of puzzle-solving and problem-defining. Moreover, it should be noted that problem-defining is much more than proposing a problem. In fact it usually consists of activities of problem-proposing (i.e. propose an initial problem), problem-refining (i.e. refine an initial problem), and problem-specification (i.e. make an initial problem into some more specific and practical problems).

Thus, my definition of exemplar is as follows:

An exemplar is a set of contextually well-defined research problems and the corresponding solutions.

First of all, I follow Kuhn in maintaining that one of the characteristics of an exemplar is to provide a problem-solution. However, one crucial difference between Kuhn's and my definition is that Kuhn implicitly assumes that a well-defined problem is already posed before an exemplar is constructed, whereas I contend that the contribution of an exemplar to the practice of science is more than a successful problem-solution. The well-defined research problems should be an essential constituent of an exemplar. In many historical cases, the introduction to the new research problem itself is a great scientific achievement. For instance, in *The Origins of Species*, Charles Darwin introduced many new research problems, which were never thought of or formulated before, like "How will the struggle for existence... act in regard to variation? Can the principle of selection, which we have seen is so potent in the hands of man, apply in nature?" (Darwin, 1999, p. 68) In history of science, new research problems usually play a vital role to guide the further practice.

Secondly, I take an exemplar as a set of research problems and their solutions rather than a single problem and its solution. The reason is that a set of problems and their solutions can better reflect the complex aspects of an exemplar as a scientific achievement. For example, we may argue that the Morgan school's research on *Drosophila* provides a problem of the patterns of inheritance of

Drosophila and its solution. However it is a fuller analysis that the Morgan school's research on *Drosophila* provides a set of well-defined research problems (e.g. what is the expected distribution of phenotypes in a certain generation? What is the probability that a particular phenotype will result from a certain mating? What is the frequency of crossing over between two given loci in the chromosomes?) and their solutions.

Thirdly, the reason why I define an exemplar as a set of “contextually” well-defined research problems and the corresponding successful solutions is that these research problems can only be well defined and understood in the context of their solutions. In the process of constructing an exemplar, problem-defining and solution-searching are not two independent activities. Rather these are two intertwined activities. Solution-searching is obviously dependent on the research problem, while the research problem, as I shall show in Chapter 5, can be redefined with the process of solution-searching such as conceptualisation and hypothesisation.

Fourthly, an exemplar should not be understood in a purely theoretical sense. No exemplar can be constructed in an armchair. Any exemplar must have some non-theoretical components.

Thus, a naïve version of the exemplar-based approach can be formulated accordingly as follows.

One should first analyse the history of a science by identifying the research problems. Then, one needs to analyse the solutions and practical efforts to seek solutions, and then provide details about how they were applied to solve the problems.

It is obvious that such an exemplar-based approach is still too vague to be helpful or instructive in analysing the history of science. In response, I have to articulate the components of the solutions of an exemplar in greater detail. However, it should be noted that I do not think that the constituents of the solutions of an exemplar can be characterised in a monistic way. Scientists solve the problems in different ways, so it would be unwise for anyone to try to summarise some

universally fundamental parts in their solutions. Therefore, what I would provide is rather a common recipe of an exemplar rather than a definition. By “a common recipe” I mean that an exemplar usually consists in such and such components, but definitely not exclusive. Here is my common recipe.

An exemplar has five main components: a vocabulary, which includes all the concepts employed in the problems and solutions; a set of well-defined research problems; a set of practical guides, which specify all the procedures and methodology as means to solve the problems; a set of hypotheses or models, which are proposed to solve the problems; and a set of patterns of reasoning, which indicate how to use other components to solve the problems.

Three points have to be added here. Firstly, these five components are intertwined. For instance, the hypotheses are often formulated on the basis of the results of the experiments by employing the concepts in the vocabulary; the experiments are usually designed and undertaken with the purpose of solving the research problems (e.g. by testing the hypotheses); the concepts in the vocabulary are understood with the help of undertaking the experiments and applying the hypotheses, and so on. Secondly, the vocabulary of an exemplar does not suggest the all the concepts in the vocabulary are first introduced by the exemplar. It is not unusual that the vocabulary of an exemplar has some pre-defined concepts. Thirdly, the hypotheses in the exemplar should not be narrowly construed as statements or propositions. Rather I refer to “hypotheses” as all kinds of theoretical constructions made by scientists. In the history, scientist use different terms to name this kind of work like “hypotheses”, “assumptions”, “principles”, “laws”, “theories”, “models”, “mechanisms”, etc.

Thus, correspondingly, the construction of an exemplary practice is a series of intertwined practices of experimentation, problem-defining, conceptualisation, hypothesisation, and reasoning. The experimentation is the practice of designing and undertaking the experiments. The problem-defining is the practice of defining and redefining the research problems. The conceptualisation is the practice of introducing a new conceptual scheme. The hypothesisation is the practice of

theoretical construction to make an explanatory and predictive machinery.⁴⁷ Again, all these practices are intertwined and cannot be understood as the independent activities of an exemplary practice.

Therefore, a common recipe for the exemplar-based approach can be summarised as follows.

In order to analyse the history of the practice of a scientific school, we first should identify the initial problem as the starting point of the research⁴⁸, and then trace the way of solving the initial problem by identifying the actual problems to be investigated and the way they occur in the practice, and analysing the process of problem-defining, conceptualisation, experimentation, hypothesisation, and reasoning involved. Then, we should detail the development of the intertwined practices in history to explore the development of a school of scientific practice.

Before ending this chapter, I find one more problem, namely the problem of the reception of an exemplary practice, to be articulated. Why are some exemplars successfully received, while others totally neglected or abandoned after the acceptance in a period? What makes those exemplar so successfully accepted? What are the characteristics shared by those successfully accepted exemplars?

It is obvious that philosophy alone cannot provide the complete and comprehensive answers to these questions. Why and when an exemplary practice is recognised and well received by a community of scientists are determined by intellectual, social, political, religious factors. My interest here is not to attempt to look for universal and comprehensive answers to these questions. Rather, I aim to identify some intellectual characteristics shared by all well received exemplary

⁴⁷ Note that I have to emphasise here that there is no universal account of theoretical construction. We have to delve into the historical context to study the process of hypothesisation. For example, some hypothesisations are better characterised as modelling, while others are better as the discovery of mechanism.

⁴⁸ Although I emphasised many times that one of the most important contributions of an exemplary practice is the definition of research problems, it is unlikely for a scientist to begin his studies without an initial problem, which was a well-defined research problem. These kind of initial problems might not be interesting at all for the subsequent development of the studies. A classical example is that the initial problem that inspired Morgan to conduct experiments on *Drosophila* was in search for an experimental approach to evolution, but he finally made a great achievement on solving the problems of *Drosophila*'s heredity. It is also likely that an initial problem is re-formulated in new terms.

practices in the history of science if there is any. I propose that all successfully accepted exemplar share (at least) two “intellectual” characteristics: repeatability and usefulness. A successfully accepted exemplary practice must be repeatable in the sense that all the practice of problem-defining, experimentation, conceptualization, hypothesisation, and reasoning can be repeatedly manipulated. On the other hand, a successfully accepted exemplary practice must be useful in the sense that some concepts in the vocabulary, some hypotheses, some research problems, some practical guides, or some patterns of reasoning of the exemplary practice can be used as tools to solve other existing problems or establish new exemplary practices. It should be noted that repeatability and usefulness are minimally necessary, rather than sufficient conditions of a successfully received exemplary practice.

Before taking an exemplar-based approach to analysing the origin of genetics and showing how the exemplar-based approach is helpful to understand the questions like Mendel’s contribution and the actual development of early genetics, I would revisit the history of genetics from Mendel to Bateson in the next two chapters.

3

Mendel's *Versuche* Revisited

Conventionally Mendel's paper *Versuche über Pflanzen-Hybriden* (1865) is regarded as the starting point of modern genetics. However, there are many disagreements on the interpretation of Mendel's paper. In particular, the objective of Mendel's paper and his contribution to the history of genetics are highly controversial. In this chapter, I aim to reinterpret Mendel's work on *Pisum*. Considering many discussions on Mendel's paper conflate Mendel's concern with his contribution, I shall break down the question concerning how to understand Mendel's work into three questions: What is Mendel's real concern in his paper? What did Mendel believe that he achieved in the paper? Can Mendel's paper be understood as a study on heredity?⁴⁹ Firstly, I shall argue that, under the influence of hybridism (especially Gärtner), Mendel's real concern in his 1866 paper is about development of hybrids in their progeny (*die Entwicklung der Hybriden in ihren Nachkommen*), rather than heredity (*Verbung*) in general. Secondly, I shall show that Mendel himself well recognised that his contribution is the discovery of the statistical regularity in the progeny of hybrids and the corresponding laws of development of hybrids as the explanans. Thirdly, I shall argue that Mendel's work cannot be construed as a study on heredity, no matter how heredity is interpreted.

⁴⁹ These three questions are not independent of each other. However, I believe that exploring these questions is helpful to understand Mendel's contribution to the history of genetics.

3.1 Gärtner's Legacy and Mendel's Real Concern

The once received understanding of Mendel's studies on *Pisum* is I believe quite familiar to most. Mendel, a nineteenth-century monk living in Brunn, now in the Czech Republic, spent eight years doing experiments on *Pisum* in his garden, and finally discovered the laws (or facts) of heredity, which lay down the foundation of the theory of Mendelian genetics. Correspondingly, Mendel's motivation of his studies on *Pisum* is implicitly assumed to be an attempt to investigate the hereditary patterns of *Pisum*. This traditional interpretation has been very influential among historians, geneticists, and philosophers (even today).

The story of Gregor Mendel is well-known. Between 1856 and 1863, he conducted extensive trials with pea plants, growing over twenty-eight thousand of them, which led him to draw up his famous Laws of inheritance. (Kingsbury, 2009, p. 142)

As a result of his research with pea plants, Mendel proposed ... a theory of particulate inheritance. A genetic determinant of a specific character is passed on from one generation to the next as a unit, without any blending of the units. This model explained many observations that could not be explained by blending inheritance. It also proved a very fruitful framework of further progress in understanding the mechanism of heredity. (Suzuki, Griffiths, Miller, & Lewontin, 1981, p. 100)

Gregor Mendel's (1822-1884) work in the 1860s on patterns of inheritance, rediscovered around 1900, provided evidence for unobservable differences among germ cells that might explain the preservation of traits. (Craver & Darden, 2013, p. 70)

The Central Terms: *Hybriden* and *Entwicklung*

However, it is not obvious to see this point given a closer look at Mendel's introductory remarks (*Einleitende Bemerkungen*).

Artificial fertilization undertaken on ornamental plants to obtain new color variants initiated the experiments to be discussed here. The striking

regularity with which the same hybrid forms always reappeared whenever fertilization between like species took place suggested further experiments whose task it was to follow the development of hybrids in their progeny.

.... That no generally applicable law of the formation and development of hybrids has yet been successfully formulated can hardly astonish anyone who is acquainted with the extent of the task and who can appreciate the difficulties with which experiments of this kind have to contend. A final decision can be reached only when the results of detailed experiments from the most diverse plant families are available. Whoever surveys the work in this field will come to the conviction that among the numerous experiments not one has been carried out to an extent or in a manner that would make it possible to determine the number of different forms in which hybrid progeny appear, permit classification of these forms in each generation with certainty, and ascertain their numerical interrelationships. It requires a good deal of courage indeed to undertake such a far-reaching task; however, this seems to be the one correct way of finally reaching the solution to a question whose significance for the [developmental]⁵⁰ history of organic forms must not be underestimated.

The paper discusses the attempt at such a detailed experiment... (Mendel, 1865, pp. 3–4, 1966a, pp. 1–2)

From the quoted passage, it seems that the inheritance of characters of *Pisum* is not Mendel's main concern. Neither the German word for "inheritance", nor for "heredity" appears in the introductory remarks. More surprisingly, they are absent in the rest of the paper, except that Mendel uses the verb "*vererbt* (inherited)" once⁵¹. In contrast, there are two other key words I found. The German word *Hybriden* (hybrids) remarkably appears 101 times. The title of the paper "Experiment on Plant Hybrids" (*Versuche über Pflanzen-Hybriden*) also suggests that Mendel's primary concern is about hybridisation rather than heredity. In

⁵⁰ In Sherwood's original translation, *Entwicklungs-Geschichte* is translated as "evolutionary history". However, I prefer to my translation as "developmental history", given the contemporary usage of "evolution". See my discussion in the section 3.1, for my reasons.

⁵¹ The original German text is "auch beschränkt sich diese Eigentümlichkeit nur auf das Individuum und vererbt sich nicht auf die Nachkommen". (Mendel, 1865, p. 14) (Sherwood's translation (1966a, p. 12): "furthermore, this peculiarity is restricted to the individual and not inherited by the offspring.")

addition, *Entwicklung* is another key word, appearing 45 times in the paper. (In most cases, *Entwicklung* is translated as development, though occasionally as formation or evolution by Sherwood.⁵²) In particular, Mendel explicitly states that the purpose of his experiments reported in the paper is to study “the development of hybrids in their progeny”. In his own words, the objective can be summarised as an attempt to formulate a generally applicable law of the *development of hybrids in their progeny* by a detailed experiment. Moreover, this can be confirmed in Mendel’s later letters to Nägeli, in which *Entwicklung* is still a central word⁵³. For example, in the first letter, Mendel introduces his work as a discovery of the laws of development.

The results which Gärtner obtained in his experiments are known to me; I have repeated his work and have re-examined it carefully to find, if possible, an agreement with those laws of development which I found to be true for my experimental plant. (Mendel, 1966b, p. 57)

Hence, if one makes a careful reading of Mendel’s paper (1865), it is beyond dispute that, literally speaking, Mendel’s concern is about the development of hybrids in their progeny, rather than the problem of heredity. However, it still remains controversial on how to interpret this objective: What did Mendel mean by “the development of hybrids in their progeny”? What is the underlying concern behind Mendel’s study of “the development of hybrids in their progeny”? Can “the development of hybrids in their progeny” be construed as patterns of inheritance? Some (for example, Brannigan, 1979, pp. 424, 449; Callender, 1988, p. 41; Corcos & Monaghan, 1993, p. 95; Monaghan & Corcos, 1990, p. 289; Olby, 1979, p. 67) strongly oppose the view that Mendel’s concern can be identified with the problem of heredity, since Mendel seems to make his motivation quite explicitly in the introductory remarks. He claimed that the problem he was trying to solve was significant “for the [developmental] history of organic forms.” (Mendel, 1966a, p. 2) Thus, based on this passage, there are some reinterpretations of Mendel’s motivation or objectivity since the late 1970s (for example, Brannigan, 1979; Olby,

⁵² See Appendix 1.

⁵³ See Appendix 2 for an exhaustive list of the usage of *Entwicklung* in Mendel’s letters to Nägeli.

1979). Robert Olby (1979) famously argues that Mendel's study on patterns of inheritance of the characters of *Pisum* is just the means to study "the role of hybrids in the genesis of new species".

Mendel's overriding concern was with the role of hybrids in the genesis of new species. Are hybrids variable or constant? – for if constant they might mark the first stage in the genesis of new species. He approached the subject with his conception of constant and independently transmitted characters. The laws of inheritance were only of concern to him in so far as they bore on his analysis of the evolutionary role of hybrids. (Olby, 1979, p. 67)

L. A. Callender (1988) considerably reinforces this bold view⁵⁴ by arguing that Mendel was in fact a proponent of the doctrine of Special Creation (i.e. the hybrids of two species are a third species), and his research on *Pisum* was an attempt to confirm it.

Mendel was an opponent of the fundamental principle of evolution itself, that is to say, of descent with modification, ... [remaining attached] to that modified form of the doctrine of Special Creation first proposed by Linnaeus in the proceeding century. (Callender, 1988, p. 41)

In comparison, Floyd Monaghan and Alain Corcos are more modest on interpreting Mendel's objective by avoiding making bold conjectures on Mendel's motivation.

[T]he real objectivity of Mendel's work was the creation of a mathematically precise science of hybridization modeled upon the physical sciences. (Monaghan & Corcos, 1990, p. 289)

In order to answer the questions and assess these interpretations, I find it necessary to delve into the historical research context of Mendel's study first and foremost.

Mendel, Hybrids, and Hybridism

⁵⁴ In fact, as Olby admits, this view is originally proposed by Callender in 1974 in his unpublished M.Phil dissertation. (Olby, 1979, pp. 57, 69n28)

Mendel's primary concern on hybridisation is also well reflected by the references he made in the paper. In the paper, there are five scholars and their works mentioned in total: Kölreuter, Gärtner, Herbert, Lecoq, Wichura, all of whom were important figures of hybridism⁵⁵, a research school in the late eighteenth- and early nineteenth-century. In Mendel's words, they all had "devoted a part of their lives to" the problem of the development of hybrids in their progeny. In particular, Carl Friedrich von Gärtner is mentioned 18 times, while Joseph Joseph Gottlieb Kölreuter 6 times.⁵⁶ What is more, in his Conclusion Remarks (*Schluss-Bemerkungen*), Mendel himself clearly identifies that his work on *Pisum* is within the "field" of the hybridist tradition, led by "two authorities" Kölreuter and Gärtner⁵⁷, and makes a lengthy comparison of his work with theirs. Therefore, I argue that the significance of hybridists' (especially Kölreuter's and Gärtner's) influence on Mendel should not be overlooked or underestimated.

Table 5

Cited Scholars in Mendel's paper (1866)	
Cited scholar	The number of occurrence
Kölreuter	6
Gärtner	18
Herbert	1
Lecocq	1
Wichura	3

The hybridists' legacy in Mendel's work on *Pisum* has been well recognised among historians.

⁵⁵ For a detailed study of the history of hybridism, see Roberts (1929).

⁵⁶ Herbert and Lecoq are only mentioned once in the Introductory Remarks as two of "numerous careful observers", while Wichura is mentioned two more times elsewhere with his work on willow. Gärtner is the most mentioned scholar in the paper and the only one mentioned with his titled book *Die Bastarderzeugung im Pflanzenreiche*. It should be noted that though Kölreuter is second most mentioned, he is only mentioned in accordance with Gärtner. This is partly why some historians suspect that Mendel did not read Kölreuter directly, but learnt his work via Gärtner's work. Nevertheless, it is obvious that Kölreuter and Gärtner have more important influence on Mendel.

⁵⁷ "A comparison of the observations made on *Pisum* with the experimental results obtained by Kölreuter and Gärtner, the two authorities in this field, cannot fail to be of interest." (Mendel, 1966a, p. 39)

Mendel was seen within the continuing tradition of plant hybridization from Koelreuter to Gaertner to Mendel. (Olby, 1979, p. 57)

[Mendel's] work was well within the tradition of the hybridists whose experiments he discussed. (Brannigan, 1979, p. 447)

However, there is still no consensus on in what sense and to what extent Mendel's work is framed by the hybridist tradition. Now it seems worth reviewing the history of hybridism briefly.

The study on plant hybrids originates from Carl Linnaeus. In 1751, Linnaeus published a short essay *Plantae hybridae*, which is regarded as "the founding document of the hybridist tradition." (Müller-Wille & Orel, 2007, p. 177) In *Plantae hybridae*, Linnaeus tries to distinguish species from accidental varieties by analysing differences in characters of plants with their reproduction and distribution over various habitats. According to him, accidental varieties are the plants with different characters "produced by soil, locality, climate." (Linnaeus, 1751, pp. 32–33; Müller-Wille & Orel, 2007, p. 179) On the other hand, species display different characters, which do not depend on those local conditions, but "on that natural law" that is, plants "celebrate their marriages and propagate their families, such that they rarely deflect to other species." (Linnaeus, 1751, p. 30; Müller-Wille & Orel, 2007, p. 179) In other words, if some plants differ in characters due to local conditions (e.g. soil and climate), these are different varieties, while if the set of characters of some plants still vary under the same local conditions; then these plants are different species. Therefore, for Linnaeus, the hybrids of two species are a third species (i.e. a truly breeding new species). (*The Special Doctrine of Creation*) Moreover, hybrids, Linnaeus contends, show a combination of paternal and maternal characters. However, Linnaeus's theory of hybridisation is highly speculative. He never conducted a number of carefully designed experiments to confirm his theory, though he did perform one (and the only one) experiment on a hybrid goatsbeard (*Tragopogon pratensis* X *T. porrifolius*) in preparation of the essay for competing a prize offered by the Academy of Sciences in St Petersburg.

In 1759, the same year when Linnaeus submitted the essay to the Academy of Sciences in St Petersburg, Kölreuter conducted his first hybridisation experiment in

the botanical garden of St Petersburg. The results of this experiment and the three further experiments in 1763, 1764, and 1766 made Kölreuter draw different conclusions from Linnaeus'. He doubted the possibility of the creation of new species by hybridisation. More specifically, Kölreuter mainly disagrees with Linnaeus on two points. Firstly, he argues that hybrids do not always display a combination of paternal and maternal characters, as Linnaeus believed. There are many blended characters found in his experiments. Secondly, he argues that true species hybrids are always sterile, which is neglected by Linnaeus. Based on the results, Kölreuter divides hybrid plants into three classes.

Since all the hybrids, which I was fortunate enough to produce and educate, have now been indicated, I want to divide them according to their different nature into the following classes, orders, genera, and species. Firstly, I divide them into three classes. To the first class belong the perfect hybrids, which originate from two or three different natural species, and from whose production own male seed was completely excluded. To the second class, on the other hand, belong the imperfect plants, which also result from two different natural species, whose production, however, involved a little bit of own male seed, aside from the alien one. The third class comprises hybrid varieties, which arise from two varieties of the same natural species, and from whose production own male seed was completely excluded. (Kölreuter, 1763, pp. 47–48; Müller-Wille & Orel, 2007, p. 183)

Two important things we can learn from this passage is that, firstly, the classification of hybrids relies on Kölreuter's distinction between species and varieties; secondly, unlike Linnaeus, Kölreuter's distinction is experiment-based. As Müller-Wille and Orel summarise, "For Koelreuter, it was the 'combination experiment' (*Verbindungsversuch*) itself that provided the 'true, certain, and infallible touchstone (*Probierstein*) of each particular species and variety'." (Müller-Wille & Orel, 2007, p. 183) In addition to Linnaeus's criterion of defining a species solely by descent, Kölreuter proposes another criterion, "fertility". He believes that hybrid species either produces no offspring or shows a significant reduction in fertility, while hybrid varieties are fertile. However, Kölreuter (1766) encountered some unexpected results in his hybridisation experiments of varieties

of garden carnation (*Dianthus hortensis*). Hybrid varieties, as assumed to display a blended form of parents, surprisingly exhibit a combination of their parental characters in various ways.

After almost ninety years, another important figure in hybridism, Gärtner adopted a new approach to investigate the problem of species/variety. For him,

The question of what distinguishes species from varieties is therefore [...] a purely biological one: a secure foundation for determining species cannot be found solely in abstraction, neither in the characters, nor in the intermediate forms, but has to be sought in reflection, that is in the individual history (*individuellen Geschichte*) of each species, its whole development (*Entwicklung*), and not in a particular aspect only. (Gärtner, 1849, p. 151; Müller-Wille & Orel, 2007, p. 187)

Note that this is the first time in the history to study the problem of species/varieties by examining “the development of various forms of plants (*die Entwicklung der verschiedenen Pflanzenformen*)”. (Gärtner, 1849, p. 293) Gärtner’s proposal was echoed by the objective of Mendel’s work seven years later. In addition, considering all of Mendel’s comparative analysis is made between these hybridist’s and his own work, I readily agree with Brannigan (1979), Callender (1988), and Olby (1979, 1985) on the point that Mendel’s objective was well within the hybridist tradition.

Though my brief account of the history of hybridism definitely fails to provide a complete and comprehensive characterization, it is still sufficient to suggest the central problems of hybridism: What distinguishes a species from a variety? Is it possible to have a new species by hybridisation? Given the central problems of hybridism, both Olby and Callender confidently argue that Mendel’s motivation of his research on *Pisum* is about the doctrine of special creation.

It is true that the problem of the doctrine of special creation is discussed in Mendel’s paper, especially in the final part of the concluding remarks.

Finally, the experiments performed by Kölreuter and Gärtner, and others on *transformation of one species into another by artificial fertilization* deserve

special mention. (Mendel, 1865, p. 43, 1966a, p. 44)

In particular, Callender (1988, pp. 54–55) is right that Mendel seems to express his position on the doctrine of special creation.

The success of transformation experiments led Gärtner to disagree with those scientists who contest the stability of plant species and assume continuous evolution of plant forms. In the complete transformation of one species into another he finds unequivocal proof that a species has fixed limits beyond which it cannot change. Although this opinion cannot be adjudged unconditionally valid, considerable confirmation of the earlier expressed conjecture on the variability of cultivated is to be found in the experiments performed by Gärtner. (Mendel, 1865, p. 46, 1966a, p. 47)

The paragraph, according to Callender, shows that Mendel conditionally accepts Gärtner's view that a species has fixed limits beyond which it cannot change.

Olby and Callender are also correct that Mendel believes that his work on *Pisum* is helpful to the problem of the transformation of one species into another by artificial fertilization.

If one may assume that the development of forms proceeded in these experiments in a manner similar to that in *Pisum*, then the entire process of transformation would have a rather simple explanation. (Mendel, 1865, pp. 43–44, 1966a, p. 44)

This corresponds well to Mendel's promise in the introductory remarks that his study on *Pisum* "seems to be the one correct way of finally reaching the solution to a question whose significance for the [developmental] history of organic forms." However, these still insufficiently show that "the developmental history of organic forms" can only be construed as the problem concerning the doctrine of special creation. Nor is it clear that the doctrine of special creation is Mendel's primary motivation. It should be highlighted that Mendel's comparative analysis in the concluding remarks is about more than the doctrine of special creation. The first half of the concluding remarks focuses on a comparison between Mendel's observation and prediction on the development of pea hybrids and Kölreuter's and

Gärtner's observations.

In addition, Mendel himself explicitly mentioned the motivation of his study of *Pisum* nowhere in the paper, except the statement that “this seems to be the one correct way of finally reaching the solution to a question whose significance for the [developmental] history of organic forms must not be underestimated.” In this statement, the indexical term “this” refers to a detailed experiment, which is sufficient to “determine the number of different forms in which hybrid progeny appear, permit classification of these forms in each generation with certainty, and ascertain their numerical interrelationships”. However, this statement is not really helpful for us to figure out Mendel's motivation, because it is just trivial if we read it with Mendel's objective in mind. As I have indicated, Mendel's objective is to study the development of hybrids in their progeny, so it seems trivial that his study would be significant for the developmental history of organic forms. Thus, on the evidence available it is not very likely that we can identify Mendel's initial motivation in 1856 precisely.

Furthermore, I do not think that what Mendel's initial motivation is, is a key question regarding the origin of genetics. Instead the objective of Mendel's paper is more important and interesting. What in fact influenced the three rediscoverers and other successors in the 1900s is what is explicit in Mendel's paper rather than the motivation behind it. Since it is beyond dispute that Mendel's real objective is about the development of hybrids in their progeny, I suggest that the next task is to figure out what Mendel meant by “the development of hybrids in their progeny”, especially the meaning of “development”.

Mendel and Gärtner on *Entwicklung*

Recently, some historians, realising the significance of *Entwicklung* in Mendel's paper, make great efforts to reconstruct Mendel's usage. Sander Gliboff (1999) argues that Mendel, under the influence of Franz Unger⁵⁸, refers “*Entwicklung*” to both “the individual ontogeny and the evolution of the lineage”.

⁵⁸ Franz Unger was the chair of Botany at University of Vienna when Mendel was a student there from October 1851 to August 1853. Mendel attended two courses (Anatomy and physiology of plants in October 1852, and Use of the microscope in April 1853) taught by Unger.

Unger used *Entwicklung* both for the growth and development of the individual plant and for changes in the flora through geological time. Indeed, he did not even consider the two processes distinct, since he viewed the plant kingdom as a developing super-organism with fossil floras as its embryonic stages. It is a mistake to assume that Mendel always meant *Entwicklung* in the sense of individual development.

In the introduction to his paper, Mendel found fault with previous hybridization work because it had failed to formulate “a generally applicable law of the development and evolution hybrids” (“allgemein giltiges Gesetz für Bildung und Entwicklung der Hybriden”)... The passage reveals Mendel’s Ungerian orientation, for he was seeking a law that governed development and evolution together. (Gliboff, 1999, p. 226)

On the basis of her textual analysis, Iris Sandler (2000) makes a more bold claim that though his usage of “*Entwicklung*” was influenced by its historical context, especially Schlediden’s definition and the nineteenth-century popular usage, Mendel’s phrase “the development of hybrid in their progeny” refers to the phenomena of transmission from generations to generations.

There is no doubt that Mendel’s focus is on the events of transmission, but he continues to think and speak and write about transmission in terms of nineteenth century development... Mendel’s intention – “to follow the development of hybrids in their progeny” – is a step-by-step description of the transmission and distribution of hybrid traits between parent and progeny. (Sandler, 2000, p. 11)

In contrast to what Campbell (1982) and Olby (1979) did, Gliboff and Sandler are correct to show that *Entwicklung* cannot be simply construed or translated as evolution without argument. They also insightfully suggest that Mendel’s usage of *Entwicklung* should have been influenced by his contemporaries and his time. However, something really important is missing from their analysis. Nobody has yet attempted to study the meaning of *Entwicklung* in Gärtner’s book, despite the fact that Gärtner was the most cited scholar in Mendel’s paper (1866). As the earlier quotation shows, Gärtner regards the development of a species as “a secure

foundation” to answer “the question of what distinguishes species from varieties”. Remember that Gärtner was the first proponent in the history of hybridism to study the problem of species/varieties by examining “the development of various forms of plants” (*die Entwicklung der verschiedenen Pflanzenformen*). What is more, *Entwicklung* really is one of the central terms in Gärtner’s 1849 book *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich*. (The term *Entwickel* appears 332 times in the book.) Therefore, considering the significance of *Entwick(e)lung* in both Gärtner and Mendel’s work and Gärtner’s great influence on Mendel, I contend that it is worth studying Gärtner’s usage of *Entwicklung* carefully for the purpose of making clear Mendel’s real concern.

In Gärtner’s book, *Entwicklung* is definitely nothing to do with evolution (or according to the 19th century terminology, transformation). Rather, it is closer to what we now refer to as individual ontogeny. In most cases⁵⁹, Gärtner designates *Entwicklung* to be the growth, or maturation of the plant, or of a specific part of the plant (e.g. ovary, embryo, and flower). Here are examples⁶⁰.

[O]n the contrary in the natural fertilization, although all parts of the female organs have not yet reached their complete development, the pollination of the stigma with their own pollen has rarely been unsuccessful.⁶¹ (Gärtner, 1849, p. 9)

If such a hybrid caused by procreation, its fruit is examined in the first period of their development in the interior, so no one can find the fertilised oaks in the same degree of development and the size.⁶² (Gärtner, 1849, p. 29)

These experiments seem to show once again that in addition to the various sight unseen the developmental state of the female organs of plants, both

⁵⁹ For an exhaustive list of Gärtner’s usage of *Entwicklung* in his book (1849), see Appendix 5.

⁶⁰ Gärtner’s book (1849) is not yet translated into English. If not indicated otherwise, all the translations of Gärtner’s text are mine.

⁶¹ “..., da im Gegentheil bei der natürlichen Befruchtung, wenn auch alle Theile der weiblichen Organe ihre vollständige Entwicklung noch nicht erlangt haben, eine Bestäubung der Narbe mit dem eigenen Pollen sehr selten erfolglos bleibt, ...” (Gärtner, 1849, p. 9)

⁶² “Wenn eine solche durch Bastardzeugung entstandene Frucht in der ersten Periode ihrer Entwicklung im Innern untersucht wird, so findet man die befruchteten Eichen nicht in gleichem Grade der Entwicklung und der Grösse.” (Gärtner, 1849, p. 29)

agents, the sunlight and the heat, (see Fig. Above, p 10) have a great influence on the course of fertilisation of plants.⁶³ (Gärtner, 1849, p. 49)

This occurs especially in the hybrids of a doubt whether even the deaf pollen possess the power to bring about the development of the outer envelopes of the fruit and the seed.⁶⁴ (Gärtner, 1849, p. 98)

At four plants of this species, which had gone up from the same seed from one and the same pod, all flowers buttons were castrated before their development and maturity of the anthers occurred at the same time.⁶⁵ (Gärtner, 1849, p. 566)

In many cases, Mendel uses the term *Entwicklung* in a similar way. For example,

A defective development of the keel has also been observed. (Mendel, 1865, p. 5, 1966a, p. 8)

In the pods first formed by a small number of plants only a few seeds developed, ... (Mendel, 1865, p. 13, 1966a, p. 11)

In addition, by reading Gärtner's book carefully, I have surprisingly found that some phrases used by Mendel are really similar to, and even closely related to those of Gärtner. What is more, Mendel's view on the existence of the law of hybrid development is very similar to Gärtner's. For instance, Gärtner strongly believes that the formation and development of hybrids are based on certain laws (*die Entwicklung und Bildung einer jeden Pflanze beruhe auf gewissen Gesetzen*), while those laws are still not yet known.

Given this original, full development, so the existence of the species conditional, relationship repealed, the deviation of a plant from its normal

⁶³ "Diese Versuche scheinen abermals zu zeigen, dass neben den verschiedenen, dem Auge unsichtbaren Entwicklungsgraden der weiblichen Organe der Gewächse, die beide Agentien, das Sonnenlicht und die Wärme, (s. oben S. 10) einen grossen Einfluss auf den Gang der Befruchtung der Pflanzen haben." (Gärtner, 1849, p. 49)

⁶⁴ "Hier tritt namentlich bei den Hybriden der Zweifel ein: ob nicht auch der taube Pollen die Kraft besitze, die Entwicklung der äusseren Umhüllungen der Frucht und der Samen zu bewirken." (Gärtner, 1849, p. 98)

⁶⁵ "An vier Pflanzen dieser Art, welche aus dem gleichen Samen aus einer und derselben Schote aufgegangen waren, wurden alle Blumenknöpfe vor ihrer Entwicklung und eingetretenen Reife der Antheren zu gleicher Zeit castrirt." (Gärtner, 1849, p. 566)

type are the necessary consequences of *the development and formation of each plant which are based on certain laws*, and these laws are in favor of the, needful to the perfect development of a plant, different ratios of exposure to the outer moments, light, moisture, soil, air quality, heat etc. Yet we certainly do not know these laws; but their existence are by no means questioned, especially since they are confirmed rather by a set of phenomena.⁶⁶ (Gärtner, 1849, p. 494)

This view is also reflected by Mendel in his introductory remarks, and strengthened in several places later.

That no generally applicable *law of the formation and development of hybrids* has yet been successfully formulated.⁶⁷ (Mendel, 1865, p. 3, 1966a, p. 2)

Anyone surveying the shades of color that appear in ornamental plants as a result of like fertilization cannot easily escape the conviction that ... development proceeds according to [certain laws]⁶⁸ [*die Entwicklung nach einem bestimmten Gesetze erfolgt*]. (Mendel, 1865, p. 38, 1966a, p. 38)

... unity in the plan of development of organic life is beyond doubt.⁶⁹ (Mendel, 1865, p. 43, 1966a, p. 43)

Thirdly, I find that there are some implicit connections between Mendel's and Gärtner's work. For instance, the objective of Mendel's paper as searching for the law of the development of hybrids in their progeny seems to follow a question

⁶⁶ "Werde dieses ursprüngliche, die vollständige Entwicklung, ja die Existenz der Art bedingende, Verhältniss aufgehoben, so sei die Abweichung einer Pflanze von ihrem Normaltypus die nothwendige Folge davon , d. i. die Entwicklung und Bildung einer jeden Pflanze beruhe auf gewissen Gesetzen, und werde durch diese bedingt, und diese Gesetze sprechen sich aus in den, zur vollkommenen Entwicklung einer Pflanze nothigen, verschiedenen Verhältnissen der Einwirkung der ausseren Momente, Licht, Feuchtigkeit, Boden, Luftbeschaffenheit, Wärme u. s. w. Noch kennen wir freilich diese Gesetze so gut als gar nicht; ihr Vorhandensein lasse sich aber durchaus nicht mehr verkennen, wir seien vielmehr durch eine Menge von Erscheinungen gezwungen, sie als vorhanden anzunehmen." (Gärtner, 1849, p. 494)

⁶⁷ "Wenn es noch nicht gelungen ist, ein allgemein giltiges Gesetz für die Bildung und Entwicklung der Hybriden aufzustellen." (Mendel, 1865, p. 3)

⁶⁸ Sherwood's original translation is that "according to a certain law", but it is in fact a mistranslation, because in Mendel's German text the plural term *Gesetze* (laws) is used.

⁶⁹ "... die Einheit im Entwicklungsplane des organischen Lebens ausser Frage steht." (Mendel, 1865, p. 43)

asked by Gärtner at the end of the book.

How do these different seeds *behave in their further development* (in 1849) with respect to the type of plants and their seed production?⁷⁰

Moreover, “the [developmental] history of organic forms” (Mendel, 1966a, p. 2) to which Mendel contends that his research on peas seems highly relevant is also an unsolved problem for Gärtner.

Because there we still lack of means, to declare in its various phases and to follow in the organism or to construct the origin and *development of the various forms of plants* from simple cell to at completed development of the perfect crop: we are not even able to determine the band, bringing the law of hybrid formation with the vegetable metamorphosis at all related.⁷¹ (Gärtner, 1849, p. 293)

Considering the similarity of the usage of *Entwick(e)lung* and the view on the law of hybrid development, and the inner connections between Mendel’s and Gärtner’s work, I wish that it is sufficient to show that Mendel’s usage of *Entwicklung* might have been inherited from (or at least largely influenced by) Gärtner’s. For anyone who is still unconvinced, there is another piece of evidence in Mendel’s paper to show that Mendel’s concern on *Entwicklung* is inherited from Gärtner’s work.

Gärtner mentions that in cases where development was regular the two parental types themselves were not represented among the offspring of the hybrids, only occasional individual closely approximating them.⁷² (Mendel, 1865, p. 40, 1966a, pp. 40 – 41)

⁷⁰ “Wie sich diese verschiedenen Samen in ihrer weiteren Entwicklung (im Jahr 1849) in Absicht auf den Typus der Pflanzen und ihrer Samenerzeugung verhalten werden.” (Gärtner, 1849, p. 680)

⁷¹ “Da es uns noch an Mitteln fehlt, die Entstehung und Entwicklung der verschiedenen Pflanzenformen von der einfachen Zelle an bis zur vollendeten Entwicklung des vollkommenen Gewächses in ihren verschiedenen Phasen zu erklären und im Organismus zu verfolgen oder zu construiren: so sind wir auch noch nicht im Stande, die Bande zu bestimmen, womit der Metaschematismus der hybriden Bildung mit der vegetabilischen Metamorphose überhaupt zusammenhängt.” (Gärtner, 1849, p. 293)

⁷² “Gärtner erwähnt, dass in jenen Fällen, wo die Entwicklung eine regelmässige war, unter den Nachkommen der Hybriden nicht die beiden Stammarten selbst erhalten wurden, sondern nur einzelne ihnen näher verwandte Individuen.” (Mendel, 1865, p. 40)

It is very clear that in this paragraph Mendel shares the usage of *Entwick(e)lung* with Gärtner. Therefore, contra Gliboff (1999), I argue that Mendel did not refer the term *Entwicklung* to both individual ontogeny and evolution. No evidence available in Mendel's publication suggests that his usage of *Entwicklung* is influenced by Unger. Even if in the introductory remarks Mendel uses the phrase "law of the formation and development of hybrids (*Gesetz für die Bildung und Entwicklung der Hybriden*)", it does not clearly suggest that *Bildung* means development while *Entwicklung* evolution. Gärtner uses *Bildung* to designate the process of formation in his book where he also frequently uses the phrase like *Samebildung* (seed-formation), *Fruchtbildung* (fruit-formation), *die Bildung des Embryo aus dem Pollen* (the formation of the embryo from the pollen). Gliboff is correct to point out that *Bildung* and *Entwicklung* have distinct meanings, but he mistranslates *Bildung* as individual ontogeny and *Entwicklung* as evolution of genealogy.

The Development of Hybrids in their Progeny and the Developmental Series (*Entwicklungsreihe*)

However, it should be emphasised that though following Gärtner's usage of *Entwicklung*, Mendel's work on *Pisum* is not about the development of hybrids. Rather it is in fact an extension of Gärtner's work. While Gärtner focused on the development of hybrids in one generation, Mendel was particularly interested in comparing the development of hybrids in different generations. More precisely speaking, Mendel particularly refers "the development of hybrids in their progeny" to "the developmental series" (*Entwicklungsreihe*) of hybrid forms in different generations (i.e. the distribution of different morphological forms). Remember Mendel's conviction that the law of development of hybrid in their progeny can only be discovered by determining the "numerical relationships of different of hybrids". He also explicitly mentions that the numerical relationships of hybrid forms are determined by observing the developmental series of offspring.

To discover the relationships of hybrid forms to each other and to their parental types it seems necessary to observe without exception all members

of the series⁷³ (*Entwicklungsreihe*) of offspring in each generation. (Mendel, 1865, p. 5, 1966a, p. 4)

Thus, Mendel's concern can also be summarised as a study on the developmental series of hybrid in different generations, where the development series means the numerical relationships of the forms of hybrids. It is evident that Mendel's major discussions in the paper are centred on the developmental series.

If A denotes one of the two constant traits, for example, the dominating one, a the recessive, the Aa the hybrid form in which both are united, then the expression

$$A + 2Aa + a$$

gives the [developmental series] for the progeny of plants hybrid in a pair of differing traits. (Mendel, 1865, p. 17, 1966a, p. 16)

When, therefore, two kinds of differing traits are combined in hybrids, the progeny develop according to the expression:

$$AB + Ab + aB + ab + 2ABb + 2aBb + 2AaB + 2Aab + 4AaBb$$

Indisputably this [developmental series] is a combination series in which the two [developmental series] for the traits A and a, B and b are combined term by term. (Mendel, 1865, pp. 20–21, 1966a, p. 20)

The difference of forms among the progeny of hybrids, as well as the ratios in which they are observed, find an adequate explanation in the principle just deduced. The simplest case is given by the [developmental series] for one pair of differing traits. (Mendel, 1865, p. 29, 1966a, p. 29)

Moreover, as we shall see in the section 2.2, all Mendel's laws are in fact about the developmental series. Therefore, I argue that the developmental series for the progeny of hybrid is Mendel's real concern.⁷⁴

⁷³ This is a major error in Sherwood's translation (Mendel, 1966a), in which *Entwicklungsreihe* is translated as series rather than developmental series in all of its 17 occurrences. (See Appendix 1) However, such a translation fails to reflect the significance of *Entwicklungsreihe* (or even *Entwicklung*) in Mendel's paper (1865).

⁷⁴ Unfortunately, partly because of the traditional mistranslation of *Entwicklungsreihe* (for example, Bateson, 1902; Mendel, 1966a), historians used to overlook the relation of "developmental series (*Entwicklungsreihe*)" and "the development of hybrids in their progeny (*die Entwicklung der Hybriden in ihren Nachkommen*)".

Furthermore, this is why Mendel explicitly identifies that his task is “to follow the development of hybrids in their progeny” rather than “to follow the development of hybrids themselves” in the introductory remarks. Thus, Mendel’s objective as looking for the law of the development (*Entwicklung*) of hybrids in their progeny is an extension of Gärtner’s research. As Müller-Wille and Orel correctly point out, “Mendel, in stating his aims, was simply taking the programme of Gärtner a step forward.” (Müller-Wille & Orel, 2007, p. 192) Therefore, it is confirmed again that Mendel’s work does not aim to investigate the hereditary patterns of peas, in contrast to what has been traditionally interpreted. His real concern is to follow and develop Gärtner’s interest in the development of the plant, where “the [developmental] history of organic forms” has been explicitly defined by Gärtner as a process from the single cell to a perfectly mature form of a plant. (Gärtner, 1849, p. 293)

Nevertheless, rejecting the traditional interpretation that Mendel’s concern is about heredity does not suggest that I would embrace the revisionist interpretation, mainly developed by Olby (1979), Callender (1988), and Di Trocchio (1991), which states that Mendel’s initial motivation or objective is about the genesis of new species by hybridisation⁷⁵. As I have argued, Mendel’s initial motivation is extremely difficult to identify while his objective should not be simply conflated with the problem of transformation of species by hybridisation.

Summary

In this section, I have shown that Mendel’s concern of his study on *Pisum* is not about heredity. Rather, by carefully analysing Mendel’s paper and its historical research context, I can now conclude that under Gärtner’s influence, Mendel’s objective is to study the development of hybrids in their progeny (or the developmental series for the progeny of hybrids). Gärtner’s influence on Mendel is reflected in both the terminological and methodological sense: Mendel followed

⁷⁵ In fact there are some differences between Olby, Callender, and Di Trocchio’s reinterpretations. For Olby, Mendel’s concern is “the role of hybrids in the genesis of new species.” (1979, p. 67) Di Trocchio goes further and more explicitly: “the original aim of Mendel’s experiments was to check whether or not new species could be produced by hybridization.” (1991, p. 507) Callender is the most bold: “Mendel was an opponent of the fundamental principle of evolution itself.” (1988, p. 41)

Gärtner's usage of *Entwicklung* and developed his study of the development of hybrids (*die Entwicklung der Hybriden*).

3.2 Mendel on his Achievement: The Ratios and Laws

In this section, I aim to reexamine what Mendel himself believed he achieved in his study of *Pisum*. More precisely speaking, I shall examine whether there is any achievements he believed that he made eventually on the study of hybrid development in their progeny.

The Conceptualisation of the Mendelian Ratios

Some historians argue that most of Mendel's work was nothing astonishingly new. Most of his work on *Pisum* was merely a confirmation of observations reported before.

Before Mendel, the component parts of Mendelism had been discovered separately, some by the plant hybridizers and some by the bee breeders. (Zirkle, 1951, p. 103)

[Mendel's] observations on segregation and independent assortment were recorded by his predecessors and the focus on inheritance ratios was pioneered by his contemporary. (Brannigan, 1979, p. 440)

However, this is definitely not what Mendel himself thought of his work on *Pisum*. In a letter to Nägeli (18 April 1867), Mendel was clear on the point that he believed that he did discover something novel.

I knew that the results I obtained were not easily compatible with our contemporary scientific knowledge. (Correns, 1906, p. 199; Mendel, 1966b, p. 60)

In fact, not only did Mendel aim to study the development of plant hybrids in their progeny, but also he believed that his work on *Pisum* eventually turns out to be an important contribution to the study of hybrid. Mendel recognised the "striking regularity" of the development of hybrids in their progeny from his experiments on *Pisum*. As I mentioned in section 1.1, when the peas differing in a pair of antagonistic traits are crossed, all the seeds obtained resemble one of the parental traits. For example, Mendel recognised that the hybrid seeds of purely bred yellow peas and green ones are all yellow. It must be emphasised that Mendel's

recognition that all the hybrids are yellow is more than a mere observation. Rather it also involves a conceptual reconstruction. Mendel denotes that yellowness in the parental peas as the dominating parental trait, which refers to the parental trait passing unchanged to all of the offspring, while greenness as the recessive parental trait, which refers to the parental trait absent in the offspring.

Moreover, when these hybrid seeds are self-fertilised, both yellow and green seeds are obtained in the offspring. And the ratio of the yellow seeds to the green ones is close to 3 : 1. Thus, it seems to Mendel that the ratio of the seeds with the dominating trait to the ones with the recessive trait is 3 : 1. It must be also emphasised that it is not obvious for Mendel to recognise those Mendelian ratios. As we can see from Table 1, though all the ratios are close to 3 : 1, it is still a novel move for Mendel to classify the morphological traits statistically. As we shall see in the section 3.1, de Vries, when undertaking the similar crossing experiments, initially failed to recognise the 3 : 1 ratio. In addition, Mendel's recognition of the 3 : 1 ratio is more than a simple approximation of the raw data. Rather it is a conceptual analysis in terms of dominance and recessiveness. Without the definition of dominating and recessive traits, the 3 : 1 ratio is unrecognisable. It is a substantial conceptual construction by Mendel to classify the morphological traits in terms of dominance and recessiveness. What is more, Mendel further reconceptualised the 3 : 1 ratio into the 1 : 2 : 1 ratio, which represents the distribution of dominating (parental), dominating (hybrid), and recessive (parental) traits.

[T]he average ratio between the number of forms with the dominating trait and those with the recessive one is ... 3 : 1.

The dominating trait can have double significance here – namely that of the parental characteristic or that of the hybrid trait. In which of the two meanings it appears in each individual case only the following generation can decide. As parental trait it would pass unchanged to all of the offspring; as hybrid trait, on the other hand, it would exhibit the same behavior as it did in the first generation. (Mendel, 1865, pp. 14–15, 1966a, p. 13)

The ratio of 3:1 in which the distribution the distribution of the dominating

and recessive traits take place in the first generation therefore resolves itself into the ratio of 2:1:1 in all experiments if one differentiates between the meaning of the dominating trait as a hybrid trait and as a parental trait. (Mendel, 1865, pp. 16–17, 1966a, p. 15)

In these paragraphs, the dominating trait is redefined. Mendel distinguishes two senses of the dominating trait. The dominating parental trait is the trait which passes unchanged to all of the offspring, while the dominating hybrid trait which would exhibit the same behaviour with the 3 : 1 ratio in its offspring, as illustrated in Figure 4, where A denotes the dominating parental trait, while Aa the dominating hybrid trait.

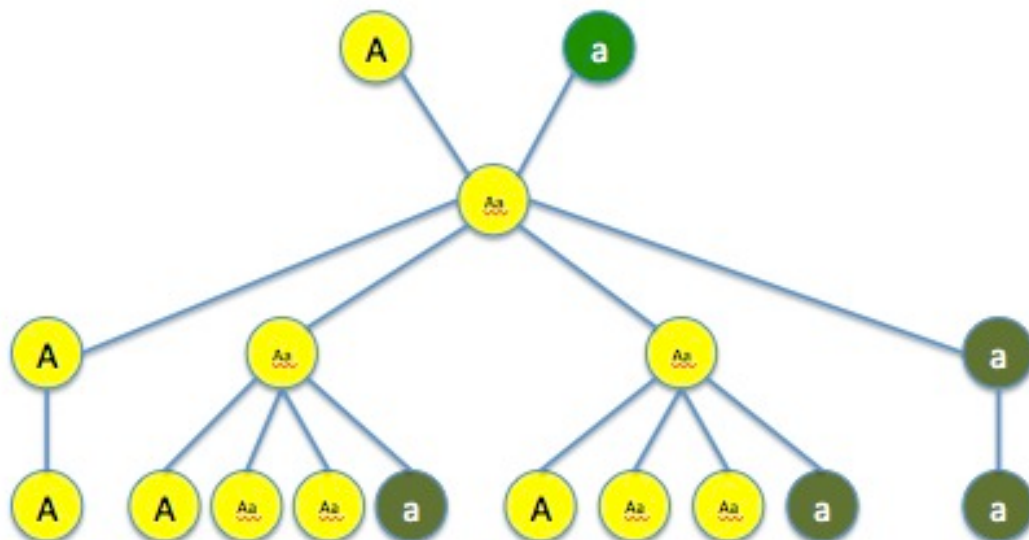


Figure 4

This redefinition is really important for Mendel. It suggests that he recognised that there is a distinction between the yellow seeds in the first generation. Some yellow seeds only produce yellow seeds, while others produce both yellow and green seeds. The former is redefined as the dominating parental trait, whereas the latter as the dominating hybrid trait. This distinction leads Mendel and his reader to recognise another “striking” regularity. Among the offspring of the peas with the dominating hybrid trait, the distribution of the dominating parental trait, dominating hybrid trait, and the recessive trait is 1 : 2 : 1 again. Based on this, Mendel formulated the law of development of hybrid that “apply to a pair of

differing traits". Thus, one significant achievement that Mendel believed that he had made was the recognition of those Mendelian ratios among the progeny of hybrids.

Mendel's Got Laws

Mendel's other achievement that he was very proud of was his discovery of the laws of hybrid development. He (1865) repeatedly emphasised that he discovered the laws of development, though he was still cautious on the universal applicability of the laws. As we can see from the following quotations:

The next task consisted in investigating whether the law of development [*Entwicklungs-Gesetz*] thus found would also apply to a pair of differing traits when several different characteristics are united in the hybrid through fertilization. (Mendel, 1865, p. 18, 1966a, p. 17)

The law of combination of differing traits [*Das Gesetz der Combinirung der differirenden Merkmale*] according to which hybrid development proceeds thus finds its basis and explanation... (Mendel, 1865, p. 32, 1966a, p. 32)

The object of further experiments will be to determine whether the law of development [*Entwicklungsgesetz*] discovered for *Pisum* is also valid for hybrids of other plants. (Mendel, 1865, p. 32, 1966a, p. 32)

Despite the many obstacles with which the observations had to contend, this experiment still establishes that development follows the same law[s]⁷⁶ [*Gesetze*] as in *Pisum*... (Mendel, 1865, p. 34, 1966a, p. 35)

But these puzzling phenomena, too, could probably be explained by the law[s]⁷⁷ [*Gesetze*] valid for *Pisum*... (Mendel, 1865, p. 35, 1966a, p. 35)

If it is assumed that development of hybrids follows the law[s] [*Gesetze*]⁷⁸ valid for *Pisum*... (Mendel, 1865, p. 39, 1966a, p. 40)

Yet even the validity of the laws [*Sätze*] proposed for *Pisum* needs

⁷⁶ This is a mistranslation of Sherwood's translation, since in the German text, the plural term *Gesetze* rather than the singular term *Gesetz* was used.

⁷⁷ Another mistranslation, see footnote 76.

⁷⁸ Another mistranslation, see footnote 76.

confirmation, and a repetition of at least the more important experiments is therefore desirable... Whether variable hybrids of other plant species show complete agreement in behavior also remains to be decided experimentally; one might assume, however, that no basic difference could exist in important matters since *unity* in the plan of development of organic life is beyond doubt. (Mendel, 1865, p. 42, 1966a, p. 43)

It has been debated how many laws Mendel discovered among historians. Müller-Wile and Orel (2007) argue that Mendel only had one law in mind, while Callender (1988) maintains that Mendel identified two laws. However, Mendel enunciates that he discovers more than one law of development in the paper (1865). As we have seen, in most places Mendel uses the plural form *Gesetze* (laws) rather than the singular form *Gesetz* (law).⁷⁹ In particular, Mendel also explicitly identified what he found in his experiments on *Pisum* is the laws of development in his letter (31 December 1866) to Nägeli.

I have repeated [Gärtner's] work and have reexamined it carefully to find, if possible, an agreement with those laws of development [*Entwicklungsgesetze*] which I found to be true for my experimental plant. (Correns, 1906, p. 195; Mendel, 1966b, p. 57)

Precisely speaking, in his paper Mendel formulates three laws of “development of hybrid”: the law of development (*Entwicklungs-Gesetz*) that “apply to a pair of differing traits (*welche nur in einem wesentlichen Merkmale verschieden waren*)” (Mendel, 1865, p. 18), the “law of combination of differing traits (*Gesetz der Combinirung der differierenden Merkmale*)” (Mendel, 1865, p. 32), and the law of “the composition of hybrid fertilizing cells (*die Beschaffenheit der hybriden-Befruchtungszellen*)” (Mendel, 1865, p. 45).

Müller-Wile and Orel (2007) believe that Mendel formulates the law of development concerning a pair of differing traits as follows:

... [O]f the seeds formed by the hybrids with one pair of differing traits, one half again develop the hybrid form while the other half yield plants that

⁷⁹ Now we can see that Sherwood's translation fails to reflect this subtle difference in some sentences.

remain constant and receive the dominating and the recessive character in equal shares. (Mendel, 1865, p. 17, 1966a, p. 15)

This statement is italicised in Mendel's original paper (1865), in which italicised terms and sentences are what Mendel attempts to emphasise. So, Mendel did seem to take it as the formulation of law of development concerning a pair of differing traits. However, from a philosopher's point of view, I regard it only as the statement of an instance of the law in the first generation of hybrids. A more general form of the law should be that the ratio of the dominating constant form, the hybrid form, and the recessive constant form in the n^{th} generation is $2^n - 1 : 2 : 2^n - 1$ under the assumption that "on the average, equal fertility for all plants in all generations, and if one considers, furthermore, that half of the seeds that each hybrid produces yield hybrids again while in the other half the two traits become constant in equal proportions." (Mendel, 1865, pp. 17–18, 1966a, p. 16) This law of development concerning a pair of differing traits is really important for Mendel, since the two other laws are formulated on the basis of it. For example, the law of combination of differing traits is about its applicability to multiple pairs of differing pairs, which is stated as follows:

The progeny of hybrids in which several essentially different traits are united represent the terms of a combination series in which the [developmental series] for each pair of differing are combined... at the same time that the behavior of each pair of differing traits in a hybrid association is independent of all other differences in the two parental plants. (Mendel, 1865, p. 22, 1966a, p. 22)

In addition, the law of composition of hybrid fertilising cells provides the "basis and explanation" of the law of combination of differing traits, as well as the law of development concerning a pair of differing traits. This law is formulated as follows.

... [P]ea hybrids form germinal and pollen cells that in their composition correspond in equal numbers to all the constant forms resulting from the combination of traits united through fertilization. (Mendel, 1865, p. 29, 1966a, p. 29)

Although Mendel does not explicitly use the term *Gesetz* to name “the assumption” about the composition of hybrid fertilising cells, there is another passage where Mendel clearly identifies his discovery of the law on the composition of cells, where he refer *Sätze* to all his laws.

Yet even the validity of the laws [*Sätze*] proposed for *Pisum* needs confirmation, and a repetition of at least the more important experiments is therefore desirable: for instance, the one on the composition of hybrid fertilizing cells. (Mendel, 1865, p. 42, 1966a, p. 43)

Though in the case Mendel used the term *Sätze* rather than *Gesetze*, the key point is that Mendel again used the plural term to identify his discovery. Therefore, in contrast to what Müller-Wille and Orel maintained, Mendel believed that he discovered the laws of development rather than the law of development.

Table 6

Mendel's Laws in <i>Versuche</i> (1865)			
Traits Level	The law of development that applies to a pair of differing traits (LDT)	The law of combination of differing traits (LCT)	
Cell Level			The law of composition of hybrid fertilising cells (LCC)

Thirdly, Mendel believes that his law on the composition of cells underlies the law of development of one pair of differing traits and the law of combination of differing traits by providing a reductionist explanation of the numerical interrelationships of the morphological traits of hybrids in their progeny.

The law of combination of differing traits according to which hybrid development proceeds thus finds its basis and explanation in the proven statement that hybrids produce germinal pollen cells that correspond in equal numbers to all the constant forms resulting from the combination of

traits united through fertilization. (Mendel, 1865, p. 32, 1966a, p. 32)

The distinguishing traits of two plants can, after all, be caused only by differences in the composition and grouping of the elements existing in dynamic interaction in their primordial cells. (Mendel, 1865, p. 42, 1966a, p. 43)

Fourthly, it is clear that Mendel's laws are all about the developmental series. For example, LDT is about the developmental series of dominating constant, hybrid, and recessive constant forms of hybrids, which is also symbolically formulated by Mendel as $A + 2Aa + a$ where A denotes the dominating constant form, Aa the hybrid form, and a the recessive constant form. Mendel's LCT is about the developmental series of the progeny hybrids which differ more than a pair of differing traits, while Mendel's LCC provides a reductive explanation of LCT and LCD. Thus, it seems to be more appropriate to call Mendel's laws "the laws of developmental series". This, again, confirms my conclusion in the section 2.1 that Mendel's concern is about developmental series of the progeny of hybrids.

Finally, Mendel believes that his laws of development, especially the law on the composition of cells, are useful to analyse and explain some unsolved problems in plant hybridism. For example, in the concluding remarks, he contends that one of "most difficult [problems] in hybrid production", that is, "transformation of one species into another by artificial fertilization", can be analysed and explained by applying his laws of hybrid development.

If one may assume that the development of forms proceeded in these experiments in a manner similar to that in *Pisum*, then the entire process of transformation would have a rather simple explanation. (Mendel, 1865, pp. 43–44, 1966a, p. 44)

In his first letter to Nägeli, Mendel explicates this project in greater detail by studying the law underlying the transformation of *G. urbanum* into *rivale* on the basis of his laws of developmental series of hybrids.

In order to determine the agreement, if any, with *Pisum*, a study of those forms which occur in the first generation should be sufficient...

Hieracium, Cirsium, and Geum I have selected for further experiments... The hybrid *Geum urbanum* + *rivale* deserves special attention. This plant, according to Gärtner, belongs to the few known hybrids which produce nonvariable progeny as long as they remain self-pollinated. To me it does not seem quite certain that the hybrid which Gärtner obtained was actually *G. intermedium* Ehrh. Gärtner calls his plant an intermediate type; this designation can not be applied without qualification to *G. intermedium*. In the transformation of *G. urbanum* into *rivale*, Gärtner states explicitly that, by fertilization of the hybrid with the pollen of *rivale*, only homogeneous offspring, which definitely resemble the paternal type, were obtained. However, we are not informed as to where this resemblance lies, and to what degree characters of *G. urbanum* were suppressed by each successive fertilization, until finally the pure *rivale* type emerged. It can hardly be doubted that this gradual transformation obeys a definite law, which, if it could be discovered, would also give clues to the behavior of other hybrids of this type. I hope to be able to get this artificial hybrid to flower next summer. (Correns, 1906, pp. 195–197; Mendel, 1966b, pp. 57–59)

This application of the laws of hybrid development echoes Mendel's promise in the introductory remarks that the discovery of the law of development of hybrids is significant for "the [developmental] history of organic forms."⁸⁰

In summary, it can be concluded that Mendel himself well recognises that his work on *Pisum* is about the development of hybrids in their progeny. For those who have not yet been convinced by my arguments and are still inclined to maintain that Mendel's concern is about heredity, one important question remains.

If Mendel's real concern would have been about heredity rather than development of hybrids in their progeny, why didn't Mendel emphasise this literally in the paper

⁸⁰ Olby (1991) provides an alternative reading of Mendel's promise. He takes the "developmental history of organic forms" as the ultimate question Mendel aims to answer in his 1866 paper. In the concluding remarks, Mendel's purpose, as explicitly stated in the opening sentence, is to compare his observations on peas with Kölreuter and Gärtner's experimental results. The problem of transformation is just one and the final one of the several comparative studies in the concluding remarks. In addition, though Mendel is explicit that the significance of his studies on peas for the developmental history of organic forms must not be underestimated, it does not imply that the developmental history of organic forms is Mendel's ultimate concern in the paper.

and his correspondence with Nägeli instead? In short, it seems to me really difficult to insist that Mendel's concern is about heredity until this puzzle is well solved.

3.3 Understanding Mendel on *Pisum*: It isn't about Heredity at all!

Even if many admit that Mendel's objective is not about heredity, some still try to argue that Mendel's work can be read as a work of heredity. Müller-Wille and Orel maintain that though Mendel's motivation cannot simply be read as an attempt to study patterns of inheritance of peas, Mendel's work is definitely Mendelian. In their words, "What Mendel achieved by his experimental analysis was a kind of anatomy of inheritance." (Müller-Wille & Orel, 2007, p. 212) One of their crucial arguments is that Mendel's approach is totally different from his predecessors Linnaeus, Kölreuter, and Gärtner. In particular, they argue that the real objective of Mendel's experiments is not about hybrids as stated in the introductory remarks. Müller-Wille and Orel claim that they find a "reformulation of the aim of Mendel's experiment". Here is the passage.

The object of the experiment was to observe [the] variations [in the progeny of the hybrid] in the case of each pair of differentiating characters, and to establish the law according to which they appear in successive generations. The experiment resolves itself therefore into just as many separate experiments as there are constantly differentiating characters presented in the experimental plants'. (Mendel, 1865, p. 7, 1966a, p. 5)

For Müller-Wille and Orel, this passage shows a shift of the aim of Mendel's work from a study of hybrids to a study of the characters of hybrids. However, I do not see this as a shift of the aim of Mendel's research. Rather, as I shall argue in detail in the section 5.2, it is just a *problem-specification*. Müller-Wille and Orel are right to point out that the subject of Mendel's research on *Pisum* is paired morphological traits of pea hybrids, but the study on the paired characters of pea hybrids is the means rather than the ends. Mendel's careful discussions on the paired characters of pea hybrids are merely the means to study the general problem of the developmental series of hybrids in their progeny.⁸¹ His ultimate concern is still about the developmental series of hybrids in their progeny. As I have cited earlier, in his first letter to Nägeli, Mendel clearly describes his achievement as finding the "laws of development". (Mendel, 1966b, p. 57) In this section, I shall argue that

⁸¹ See more in-depth discussion in Chapter 5.

Mendel's work on *Pisum* cannot be understood as a work of heredity, whether in the 19th century or 20th century sense.

Mendel: A Geneticist in the 20th Century sense?

There are two other lines of argument for the view that Mendel's research can be understood as a work of heredity. Firstly, some (for example, Hartl & Orel, 1992; Sandler & Sandler, 1985) argue that there are premature versions of the laws of segregation and of independent assortment in Mendel's paper. The problem that Mendel was studying is in fact the patterns of inheritance, from a contemporary point of view. So Mendel is a geneticist in the 20th century sense. The first line of argument has been widely discussed. Olby makes a systematic argument against this view by rejecting that there is any explicit formulation of the laws of segregation and of independent assortment.

Mendel did not have the conception of pairs of factors or elements determining his pairs of contrasted characters... There is no case for the view that Mendel conceived of paired hereditary particles equivalent to the alleles in classical genetics. He went no further than postulating one kind of element in the germ cell for any one trait.

... The cell theory of fertilization... in Mendel's Versuche... did not serve as a basis for cytological theory about hereditary determinants. (Olby, 1979, p. 67)

Though Olby is right that Mendel's laws of hybrid development are conceptually different from the so-called Mendel's laws of inheritance in the 20th century, it is hardly a serious challenge to the view that Mendel's work can be read as a work of heredity in the 20th century sense. Olby's argument can be countered by arguing that Mendel's laws of hybrid development are just a premature version of the theory of Mendelian genetics. Thus, it seems still plausible to understand Mendel's work as a study of heredity.

Nevertheless, this defence is not conclusive. I wonder to what extent Mendel's work can be understood as a work of heredity. As I have asked in the section 1.2, if Mendel's laws can be understood as a version of the theory of Mendelian genetics,

what underlies the relation between Mendel's version and the later versions? Why should we believe, say, that Mendel's laws and de Vries' law of segregation are different versions of a single theory rather than different theories?

As a response, Raphael Falk and Sahotra Sarkar (1991), accepting that there are substantially conceptual differences between Mendel's laws and the laws of inheritance, argue that Mendel was studying the problem of heredity in terms of development.

Indeed, as Olby ... has observed, Mendel phrased his problem in terms of the formulation of hybrids and their progeny. The reason for this is the historical context: in the first half of the nineteenth century, Moravia was a center of intensive breeding activity which provoked considerable interest in intellectual circles ... The breeding methods of Robert Blakewell that were imported from England and promoted by Geisslern (known as the "Moravian Blakewell") were those of the production of hybrids between divergent strains showing desired traits and transmit them to the progeny over several generations. A difficulty that arose was that the traits did not breed true. When Mendel addressed such problems he was, therefore, directly addressing a problem of heredity. Conceptually, moreover, it could not have been otherwise. If hybrids are formed through reproduction, and pass traits on (with whatever success) through reproduction, and these are the traits being studied, what is being studied, *ipso facto*, is the inheritance of traits. The problem of inheritance is, in some sense, more general than the problem of hybridization. But that hardly means that studying hybridization is not studying inheritance. (Falk & Sarkar, 1991, p. 448)

At first glance, Falk and Sarkar's argument seems to be quite promising. It not only defends that Mendel's work is about heredity by identifying the problem of heredity, but also answers a question I asked at the end of last section: why didn't Mendel mention heredity in his paper? Unfortunately, the argument is flawed in many ways. The biggest problem is the circularity. Falk and Sarkar are looking at Mendel's problem with a 20th century prejudice. In other words, Mendel's problem was construed with a contemporary understanding of the problem of inheritance.

Falk and Sarkar's argument can be reformulated as follows:

P1. Transmission of morphological traits is a central problem in the science of heredity.

P2. Mendel was studying transmission of the morphological trait of *Pisum* in terms of development.

C. Therefore, Mendel's work can be understood as a work of heredity.

However, I have to warn that our understanding of the problem of inheritance is heavily influenced by Mendel's work. The definition of the problem of inheritance is indebted to Mendel's work. Under the influence of Mendel's focus on transmission of morphological traits, geneticists in the early 20th century began taking transmission as a central research problem in the study of heredity, which consists in our current understanding of the science of heredity. Therefore, it is circular to show that Mendel's work is about heredity by arguing that Mendel's problem is similar to the problem of transmission inheritance today!

In addition, there are two minor problems. Firstly, Falk and Sarkar's argument relies on a vague claim that Mendel's work was provoked by the studies of breeding in Moravia. Though I have no objection to the view that Mendel was more or less influenced by the breeding research in Moravia, it is unclear to what extent Mendel's problem was framed by it. There is so little written evidence to show that Mendel's study on *Pisum* was motivated by the studies of breeding in Moravia in the first half of the 19th century.⁸² Secondly, I have no idea of in what sense the problem of inheritance is more general than the problem of hybridisation. If it means, as implicitly suggested by Falk and Sarkar, that the problem of hybridisation is part of the problem of inheritance. It is definitely not the case in the 19th century. There is little evidence to show that there is correspondence between plant hybridists (e.g. Kölreuter and Gärtner) and sheep breeders in Moravia (e.g. Napp and Nestler). As Orel (1996, p. 34) points out, Rudolf Wagner (1853, p. 1018) was the first 19th century naturalist who explicitly suggested that plant hybridisation can be useful to study heredity. However, I am really sceptical on whether Mendel

⁸² This point will be discussed in greater detail later.

might have ever been influenced by Wagner's suggestion. Thus, I conclude that it is too arbitrary to argue that, for Mendel, the problem of hybridization is part of the problem of inheritance.

To sum up, I argue that Mendel's work cannot be understood as a work of heredity in the 20th century sense.

Mendel: A Geneticist in the 19th Century sense?

Another line of argument (for example, Orel & Wood, 1998; Orel, 1998) for the view that Mendel's research can be understood as a work of heredity is as follows: In the first half of nineteenth-century there are lively discussions on heredity in Brünn, Moravia, where Mendel was living. The interest of heredity arose from the study of sheep breeding. The notion of *genetische Gesetze* (genetic laws) was first introduced in 1818 to describe the patterns of inheritance in animals by Count E. Festetics. Since 1827, the word *Vererbung* (heredity) had been widely used to describe the transmission of different traits. J. K. Nestler (1783-1841), Professor of Agriculture, Science and Natural History at the Moravian University of Olomouc, and F. C. Napp (1792-1867), abbot of the Augustinian monastery in Brünn, were two leading figures in the study of heredity at that time. Soon F. Diebl, professor of the Philosophical Institute, introduced Nestler's teaching on breeding and heredity into Brünn. It is argued that Mendel must have known the context, given the evidence that Napp was Mendel's mentor, and Mendel attended Diebl's lectures. So Mendel was studying heredity in the 19th century sense.

Orel, a strong proponent of this view, reinforces this view by arguing that a key term in Mendel's paper *Entwicklungsgeschichte* (the developmental history) should be identical with *Vererbungsgeschichte* (the history of heredity).

At that time prominent sheep breeders in Moravia had kept forty years of stock registers with wool sample cards. Nestler called on them to take part in the elaboration of the principles of rational breeding to answer the key question: "What noticeable success in heredity can be achieved when rams and ewes with equal or unequal traits are paired?" The breeders were asked to examine these old family registers to investigate the history of heredity

(*Verebungsgeschichte*) of the best stock animals in their offspring from the top downward or their developmental history (*Entwicklungsgeschichte*) in their ancestors from bottom upward. From this investigation Nestler expected valuable material for the theory of breeding. The term *Entwicklungsgeschichte* was for him the other side of the same coin, of *Verebungsgeschichte*. (Orel, 1998, p. 297)

Emphasising the significance of his research approach from the view point of “*Entwicklungsgeschichte* of organic forms”, Mendel could have had in mind Nestler’s understanding of the history of heredity. (Orel, 1998, p. 299)

I agree with Orel that the problem of heredity was important in the context of animal breeding in Moravia. As Wood and Orel point out,

The big problem facing [breeders in Moravia], ... was the absence of a theory of inheritance. In 1836 Napp stated his opinion that the problem could be explained only by seeking its physiological basis, i.e. by discovering the nature and behaviour of whatever it was that was transmitted at fertilisation. When discussion on this topic continued in the following year, he formulated the key research question ‘what is inherited and how?’ (Wood & Orel, 2005, p. 268)

There are many discussions on *Vererbung* (heredity) in the literature of animal breeding in Moravia in the first half of the 19th century (for example, Nestler, 1837). It is also plausible to postulate that Mendel might have known the work of *Vererbung* (heredity) by Nestler, Napp, Diebl, etc, through either his personal acquiescence with Napp or his study under Diebl.

However, it is still unknown to what extent Mendel was influenced by these studies on heredity: Did Mendel regard the problem of heredity as an interesting problem to study? Given the evidence we have so far, it is too bold to infer that Mendel’s research on the development of plant hybrids is a means to studying the problem of heredity. No direct evidence shows that Mendel’s paper is related to *the problem of heredity* studied by Nestler and Napp. Otherwise, why didn’t Mendel mention their works in the paper? Why didn’t Mendel even suggest the potential

contribution made by his experiments on *Pisum* to the problem of heredity? Why didn't Mendel make a comparison between his observation on peas and the experimental results obtained by Nestler or other breeders in the concluding remarks, as he did with Kölreuter and Gärtner?

In addition, Nestler's belief that (*Verebungsgeschichte*) the history of heredity can be studied by means of studying *Entwicklungsgeschichte* (the developmental history) confirms a fact that *Entwicklung* (development) is an independent and important research problem in the first half of the 19th century. Given the significance of *Entwicklung* in Gärtner's research as I have pointed earlier, we can see that the study of *Entwicklung* has many potential utilities in Mendel's time. And this further confirms my conclusion that Mendel's ultimate concern was about the problem of development (*Entwicklung*).

Therefore, I contend that no matter how genetics or the study of heredity is understood in the historical context, Mendel is definitely not a geneticist in the sense that he aims to study heredity, or his work is about heredity. We should not overestimate nor underestimate Mendel's contribution to the history of genetics.

Summary

In summary, as I have shown, the traditional understanding of Mendel's contribution as the discovery of the laws of heredity was seriously challenged in the late 1970s. Some (for example, Callender, 1988; Olby, 1979) develop the revisionist interpretation by postulating that Mendel's real concern is about the genesis of new species by hybridisation. Recently Müller-Wille and Orel (2007) try to reconcile the two views by arguing that though Mendel's work on *Pisum* is oversimplified by the traditional interpretation, it is right to maintain that Mendel's work is about inheritance. However, the debate is murky especially because it fails to distinguish how to understand Mendel's contribution from what Mendel's objective is, or what Mendel's understanding of his own work was. I revisit Mendel's work on *Pisum* by focusing on three questions: What is Mendel's real concern in his paper *Versuche über Pflanzen-Hybriden* (1866)? What did Mendel believe that he achieved in the paper? Can Mendel's paper be understood as a study on heredity? And my answers are

1. Mendel's real concern in his paper *Versuche* is not about heredity. Rather, under Gärtner's influence, it is about the developmental series of hybrids in their progeny.
2. Mendel himself confirmed in the 1866 paper and his correspondence with Nägeli that his key contribution is to recognise the striking ratios among the progeny of hybrids and to discover the laws of development of hybrids.
3. Mendel's work on *Pisum* cannot be understood as a study on heredity, whether is interpreted in the 19th century or 20th century sense.

Although not all of these answers are completely new, I have tried to provide new arguments to support these. In particular, I strengthened the view that Mendel's concern was about the developmental series of hybrids in their progeny by showing Gärtner's influence on Mendel's work both methodologically and terminologically.

4

Demystifying the Rediscovery Story

As I have argued in the last chapter, Mendel's work on *Pisum* is not about heredity and cannot be understood as a study on heredity, then how should we reassess the significance of Mendel's work? What role did Mendel's work play in the origin of Mendelism at the turn of the 20th century? In order to find answers to these questions, I find it necessary to reexamine the fate of Mendel's work from 1866 to 1900 at first. In this chapter, I aim to reshape the history of the "rediscovery" story by examining the literature and material critically. Firstly, I shall show that none of the three rediscoverers' work is an independent activity in the sense that all the rediscoverers, namely, de Vries, Correns, and Tschermak, were led to the rediscovery by reading Mendel's paper (1865). Secondly, I shall argue that due to the substantial differences of their conceptual framework, there is no "rediscovery" at all. The traditional "rediscovery" characterisation oversimplifies the history of the birth of genetics around 1900 and fails to capture the practice of de Vries, Correns, and Tschermak accurately.

4.1 The Problem of Independence

We may all hear the famous story that Mendel's study on *Pisum* was hardly noticed until 1900 when de Vries, Correns and Tschermak independently re-discovered it. Ernst Mayr's neat summary is such a typical account:

[I]n the spring of 1900 ... [t]hree botanists – de Vries, Correns, and Tschermak – within a period of a few months published statements that they had independently discovered certain laws of inheritance, only to find, when checking the literature, that Mendel had anticipated them by thirty-five years. (Mayr, 1982, p. 727)

The rediscovery story consists of two theses: Mendel's work was neglected until 1900 (the long-neglect thesis); and in 1900 de Vries, Correns and Tschermak rediscovered Mendel's "laws" independently in the sense that they all happened to read Mendel's paper after the completion of (at least the majority of) their research (the rediscovery thesis). The rediscovery thesis was originally kept by all three rediscoverers' advocacy in their papers published in a German journal *Berichte der deutschen botanischen Gesellschaft* in 1900.

This important treatise [i.e. Mendel's paper (1866)] is so seldom cited, that I myself for the first time came to know about it after I had closed the majority of my experiments, and had derived therefrom the principles contributed in the text. (de Vries, 1900a, p. 85 n1, 1966, p. 110 n6)

When I discovered the regularity of the phenomena, and the explanation thereof... the same thing happened to me which now seems to be happening to de Vries: I thought that I had found something new. But then I convinced myself that the Abbot Gregor Mendel in Brunn, had, during the sixties, not only obtained the same result through extensive experiments with peas, which lasted for many years, as did de Vries and I, but had also given exactly the same explanation, as far as that was possible in 1866. (Correns, 1900, p. 158, 1966, pp. 119–120)

Correns has just published experiments, which also deal with artificial hybridization of different varieties of *Pisum sativum* and observations of the hybrids left to self-fertilization through several generations. They confirm, just as my own, Mendel's teachings. The simultaneously "discovery" of Mendel by Correns, de Vries, and myself appears to me especially gratifying. Even in the second year of experimentation, I too still believed that I had found something new. (Tschermak, 1900b, p. 239, 1950, p. 47)

However, both of the long-neglect and rediscovery theses have been heavily criticised by historians. Some studies (for example, Olby, 1985, pp. 219–234; Orel, 1996, pp. 275–279; Weiling, 1991, pp. 10–11) have shown that there are at least a dozen references to Mendel’s work before 1900. In particular, Mendel’s work was carefully studied and discussed by C. A. Blomberg (1872) and I. F. Schmalhausen (1874) in their theses. So, it is clearly not the case that Mendel’s work was completely neglected or unknown in academia. The long-neglect thesis is not well established. On the other hand, the rediscovery thesis was also seriously challenged. The major line of criticism is to question the independence of the rediscovery. During the months of March and July, in 1900, de Vries, Correns, and Tschermak published five articles on the rediscovery of Mendel’s work on *Pisum*. However, I shall show conclusively in this section that none of these publications can be legitimately regarded as an “independent” rediscovery of Mendel’s work. In other words, I shall argue that all the three rediscoverers had already read Mendel’s paper (1865) before the completion of (at least the majority of) their research, and Mendel’s paper played a vital role in the research published in the “rediscovery” papers.

Table 7

The Rediscoverers’ Publications on “Rediscovery” in 1900	
Author	Paper
Hugo de Vries	Sur la loi de disjonction des hybrides, <i>Comptes Rendus de l’Academie des Sciences (Paris)</i> , 130, pp. 845-847. (Published on March 26, 1900.)
	Das Spaltungsgesetz der Bastarde (Vorläufige Mittheilung), <i>Berichte der deutschen botanischen Gesellschaft</i> , 18(3), pp. 83-90. (Received for publication, on March 14, 1900; Published on March 30, 1900.)
	Sur les unités des caractères spécifiques et leur application à l’étude des hybrides, <i>Revue générale de botanique</i> , 12, pp.257-271. (Dated on March 19, 1900; Published on July 15, 1900)

	Über erbungleiche Kreuzungen (Vorläufige Mittheilung), <i>Berichte der deutschen botanischen Gesellschaft</i> , 18(9), pp. 435-443. (Published on November 30, 1900; Received for publication November 21, 1900.)
Carl Correns	G. Mendels Regel über das Verhalten der Nachkommenschaft der Rassenbastarde, <i>Berichte der deutschen botanischen Gesellschaft</i> , 18(4), pp.158-168. (Dated April 22, 1900; Received for publication, on April 24, 1900; Published on April 27, 1900.)
Erich von Tschermak	Über künstliche Kreuzung bei <i>Pisum sativum</i> , <i>Berichte der deutschen botanischen Gesellschaft</i> , 18(6), pp.232-239. (Received for publication, on June 2, 1900; Published on June 29, 1900.)
	Über künstliche Kreuzung bei <i>Pisum sativum</i> , <i>Zeitschrift für das landwirtschaftliche Versuchswesen in Oesterreich</i> , 3, pp. 465-555. (Submitted on January 1, 1900)

De Vries' Rediscovery and Bailey's work

As shown in the Table 7, de Vries' "Sur la loi de disjonction des hybrides" (1900c) was the earliest published "rediscovery" paper. Surprisingly, de Vries did not give Mendel any credit for the law of segregation of hybrids. Nor did he even mention Mendel in this French paper. In contrast, four days later, de Vries' another paper "Das Spaltungsgesetz der Bastarde" (de Vries, 1900a) was published in German, in which he acknowledged Mendel's priority as the discoverer of the law of segregation of hybrids.

These two statements [i.e. the law of segregation of hybrids], in their most essential points, were drawn up long ago by Mendel for a special case (peas). (de Vries, 1900a, p. 85, 1966, p. 110)

From these and numerous other experiments I draw the conclusion that the law of segregation of hybrids as discovered by Mendel for peas finds very

general application in the plant kingdom... (de Vries, 1900a, p. 90, 1966, p. 117)

It is a bit confusing that in two papers on the law of segregation both published in March, 1900, de Vries treated Mendel so differently. Why did he make no mention of Mendel in the French paper at all? One suspicion is that de Vries intended to suppress Mendel's priority at first, but had to make a reference after he realised that Correns also knew and appreciated Mendel's work. Despite a lack of direct evidence, it was once widespread and persistent. Perhaps, as Sturtevant comments, "[this suspicion] cannot be accepted as established but seems to be the simplest interpretation of the puzzling facts." (Sturtevant, 1965, p. 28) On the other hand, it can also be argued that de Vries came to know Mendel's paper after the submission of the first paper (de Vries, 1900c), and then added the reference to Mendel in the German paper.⁸³

Though never giving an explanation of this puzzling fact, de Vries was very explicit on his independence of the rediscovery of the law of segregation in the German paper.

... I first learned of [the existence of Mendel's paper] after I had completed the majority of my experiments and had deduced from them the statements communicated in the text. (de Vries, 1900a, p. 85 n1, 1966, pp. 110, n6)

Unfortunately, such a statement is too brief to be informative. Except for the confirmation that he read Mendel's paper after his proposal of the laws, de Vries fails to explicitly indicate the date of his first reading of Mendel's paper or the

⁸³ This explanation is consistent with Stomps' memoir (1954), which I shall discuss in detail later. However, it is not very convincing. Firstly, though it is not clear how long there was between de Vries' submission of the first French paper (de Vries, 1900c) and the German paper (de Vries, 1900a), given the fact that the French paper was published only five days earlier than the German paper, it is not very likely that de Vries first read Mendel's paper in the interval between his two submissions. Secondly, in 1900 some realised that de Vries must have known Mendel's paper by reading his French paper. Correns and Tschermak are among them. Tschermak wrote in his letter to Roberts in 1925: "In the beginning of April 1900, I received from Hugo de Vries, whom I visited from Ghent in the year 1898, the article 'Sur la loi de disjonction des hybrides' (March 26, 1900), in which De Vries, on pages 1-2 says: 'In the hybrid the simple differential character of one of the parents is then visible or dominant, while the antagonistic character is in the latent or excessive state.' I read this sentence with the greatest interest, but also, frankly stated, with consternation, for it was now quite clear to me that De Vries must also know the work of Mendel, although it was not cited in this paper." (Roberts, 1929, p. 346)

source that led him to it. Twenty-four years later, in a letter to H. F. Roberts, de Vries made a more detailed memoir by suggesting that his first reading happened sometime after 1895.

In 1893, I crossed *Oenothera lamarckiana* with *O. lam. brevistylis*, and found their progeny to be uniform, and true to the specific parent in 1894, but splitting in the second generation 1895, giving 17-26 individuals with the recessive character (Mut. The. II, p.157). Many other species were tried with the same result, and dihybrid crosses showed the laws of chance to be valid for them also. After finishing most of these experiments, I happened to read L. H. Bailey's 'Plant Breeding' of 1895. In the list of literature of this book, I found the first mention of Mendel's now celebrated paper, and accordingly looked it up and studied it. (Roberts, 1929, p. 323)

However, this account is somehow inconsistent with what de Vries wrote in an earlier letter to Bailey in 1905 or 1906, in which he claimed that he was led to Mendel's work by Bailey's paper (1892).

Many years ago you had the kindness to send me your article on 'Cross-breeding and Hybridizing' of 1892; and I hope it will interest you to know that it was by means of your bibliography therein that I learnt some years afterwards of the existence of Mendel's papers, which now are coming to so high credit. Without your aid I fear I should not have found them at all. (Bailey, 1915, pp. 155, n1)

By checking Bailey's book (1895), I find it clear that de Vries could not have learnt Mendel from that book, since there is no bibliography in that edition of the book. As Bailey himself correctly pointed out,

The essay, "Cross-breeding and Hybridizing," formed Chapter II of the old "Plant-Breeding" [the 1895 version]; but the bibliography that accompanied it was not reprinted until the second edition of the book. (Bailey, 1915, pp. 155, n1)

Bailey's book *Plant-Breeding* was first published in December 1895, and then reprinted three times before 1900: in April 1896, in August 1897, and in October

1897 respectively. My examination confirms that none of these versions include a bibliography, though Mendel was mentioned once in each version. The earliest reprint, which included the reference to Mendel's paper (1865), was the one published in March 1902⁸⁴. Therefore, I can conclude for sure, along with Zirkle's observation (1968), that de Vries could not have first learned of Mendel's paper from Bailey's book *Plant Breeding*.

However, I still have to emphasise that the possibility that de Vries first knew Mendel's paper from Bailey's paper *Cross-Breeding and Hybridizing* (1892) is not excluded. In addition to the version of Bailey's 1902 paper published by the rural library dated April 1892, which I found from archive.org, there is the other version⁸⁵, which was published by Wright & Potter Printing Co., State Printers dated January 1902. (See Appendix 3) There are some minor differences on the content between these two printings. The most significant difference is that in the rural library printing, Mendel's paper (1865) was in the bibliography on the page 32, while in the Wright & Potter printing, there is no bibliography included. Thus, there was no mention of Mendel's paper in the Wright & Potter printing. So, if de Vries had had a copy of the rural library printing, it remains the possibility that de Vries' first learning of Mendel's paper was from Bailey's 1902 paper.

Table 8

de Vries' claims on his "Rediscovery" story			
Source	Year/Source of First Reading	Year of Proposing the Law	Notes
"Das Spaltungsgesetz der Bastarde" (de Vries, 1900a)	After 1896	1896 (after the experiment on <i>Papaver somniferum</i>)	
"Sur les unités des caractères spécifiques et leur	After 1896	1896 (after the experiment on <i>Papaver</i>	

⁸⁴ Mendel's paper (1865) was included in the bibliography of Bailey's book (1902) on page 297. This is also what Bailey refers the second edition to. (Bailey, 1915, p. vi)

⁸⁵ I would like to thank Michael Buttolph for pointing out the existence of Wright & Potter printing and sending me an electronic copy of it.

application à l'étude des hybrides" (1900d)		<i>somniferum</i>)	
de Vries' letter to Bailey in 1905 or 1906	Some years after 1892 / Bailey's paper (1892)		There are two printings of Bailey's 1892 paper, only one of which included Mendel's paper in the bibliography.
"The Origin of the Mutation Theory" (1917)		After the experiment on <i>Papaver somniferum</i>	
de Vries' letter to Roberts on December 18, 1924	After 1895 / Bailey's book (1895)	After the experiments, especially including the one on <i>Oenothera lamarckiana</i>	No reference to Mendel in Bailey's book (1895)

Stomps on De Vries' Rediscovery

Interestingly, Theodoor Stomps (1954), a student and assistant of de Vries, tells us a different story.

Thereupon de Vries undertook his experimental work in the garden, with the result that a long series of genetical papers already appeared before 1900. He made numerous crosses between species and varieties and, being unaware of the existence of Mendel's paper, "Versuche über Pflanzenhybriden," quite independently discovered the formula, which we now know as Mendel's law. In 1900, at just the time he was about to publish the results of his experiments he received a letter from his friend Professor Beyerinck at Delft, reading thus: "I know that you are studying hybrids, so perhaps the enclosed reprint of the year 1865 by a certain Mendel which I happen to possess, is still of some interest to you." De Vries read the paper

and found that the results of his experiments, which he had believed to be quite new, had already been reported 35 years before. And it goes without saying that in his first article referring to the subject under discussion, "Das Spaltungsgesetz der Bastarde," received by the editorial staff of the Deittsche Botanische Gesellschaft on the 14th of March and published on the 25th of April 1900, the work of Gregor Mendel was accurately mentioned. This then is the true story of the rediscovery of Mendel. I once asked De Vries whether he could remember the precise moment at which he discovered Mendel's now famous paper, and he personally related the story to me. (Stomps, 1954, p. 294)

Stomps' account is different from de Vries' own in two important places. Firstly, Stomps explicitly indicates that de Vries' first reading happened in early 1900, just before the submission of his German paper (de Vries, 1900a). Secondly, de Vries was led to Mendel's paper by Beijerinck's letter rather than by Bailey's work. Stomps' account is quite favourable among historians (for example, Campbell, 1980; Corcos & Monaghan, 1985; Meijer, 1985; Zirkle, 1968), though some of them did not exclude the possibility that de Vries read Mendel's paper without understanding it before 1900. However, I have three main doubts about Stomps' account.

Firstly, what makes Stomps convinced that his account is "the true story" is that this was what de Vries told him personally. Unfortunately, as seen from de Vries' own inconsistent accounts, de Vries' memory was not very reliable. Even if Stomps tells the truth, it is exactly what de Vries told him on "the precise moment at which he discovered Mendel's now famous paper", why should we give the privilege to this account? Furthermore, I do not see why Stomps' memory of de Vries' memory of his first reading of Mendel's paper is more reliable than de Vries' own memory.

Secondly, Stomps said little on the Beijerinck's letter. As Onno Meijer insightfully points out, "Stomps seems to have quoted [Beijerinck's letter] literally, and one wonders why he did not give the date of the letter." (Meijer, 1985, p. 194 n35) What is worse, according to Meijer's investigation, Beijerinck's letter to de Vries, mentioned by Stomps, was not found in the Stomps archives at the Hugo de Vries

Laboratorium. In addition, if de Vries did have such a letter from Beijerinck, and did first learn of Mendel's paper from this letter, why did he not say anything about this in these paper (for example de Vries, 1900a, 1900d) in 1900 when the memory should be still refresh?⁸⁶ Stomps' account seems even more dubious, given the fact that de Vries never mentioned Beijerinck in his own accounts. What is more, had de Vries first known Mendel's paper from Beijerinck's letter, it would be better for him to admit it. Given his account that he discovered the law of segregation independently in 1896⁸⁷, it would be a much better way to show his independence of the rediscovery than to vaguely suggest his learning was from Bailey's work.

Thirdly, Stomps did not provide more detailed information on when and where the conversation took place. I find it reasonable to doubt the accuracy of Stomps' account. Therefore, I argue that Stomps' account cannot be more reliable than de Vries' ones, though I would not dismiss all of Stomps' account⁸⁸.

De Vries' Rediscovery and the Experiment on *Papaver somniferum*

As far as I examined these accounts, all I can conclude at this moment is, though not very interesting to many who are familiar with the literature, that de Vries' first reading of Mendel's paper was between April 1892 and March 1900. In order to further investigate de Vries' independence of the rediscovery, I shall then examine whether de Vries' first reading of Mendel's paper happened after his completion of the majority of the experiment and the proposal of the law. First of all, it seems necessary to figure out when de Vries first independently observed the important 3 : 1 ratio and formulated a Mendelian explanation.

In the end of his other 1900 French paper "Sur les unités des caractères spécifiques et leur application à l'étude des hybrides" (1900d), de Vries also asserts his

⁸⁶ Meijer's explanation of this puzzling fact is that "there is some evidence of animosity between Beijerinck and De Vries at the time." (Meijer, 1985, p. 194) However I find this explanation implausible. Meijer is vague on when there is animosity between Beijerinck and de Vries. If Beijerinck had sent de Vries a reprint of Mendel's paper in 1900, it seems obvious that they were in a good friendship at that time. It is puzzling why de Vries did not mention this in any of the 1900 papers, especially given that admitting Beijerinck's letter would not undermine his independence claim.

⁸⁷ See Table 8 and the quotation in the following pages.

⁸⁸ I shall argue later in this section that de Vries' first good reading of Mendel's paper happened around 1900, which is closer to the time provided by Stomps than by de Vries.

independence of the rediscovery by indicating that his proposal of the law of segregation was based on the experiment on *Papaver somniferum* (opium poppy).

This law [i.e. the law of segregation of hybrids] is not new. It was stated, for a particular case (peas), thirty years ago. This is Gregor Mendel who formulated it in a paper entitled "Versuche über Pflanzen-Hybriden" in the journal *Verhandlungen des naturforschenden Vereins Brünn* (T IV, p. 1), 1865. Mendel deduced the consequences not only for monohybrid, but also for di-polyhybrid.

This memoir, too good for its time, was disregarded and forgotten. We find rare citation, and then only for accessories observations. Also do I read my memoir after having completed the most essential part of the experiments cited in this article, especially after finding the proof of principle by the fourth year of cultivation (1896) of my cross of poppy.

However, I wish that I had shown that Mendel's law not only is applied to peas, but also it is applicable to all true hybrids.⁸⁹ (de Vries, 1900d, p. 271)

As we can see, this account is consistent with his other accounts on the time of his first reading, that is, some years after 1892. In addition, in regarding when and how he derived the law, this account is also consistent with de Vries' statements in German paper (de Vries, 1900a) and his book *Die Mutationstheorie* (1903).

I carried out this experiment in 1896 with *Papaver somniferum* Mephisto × Danebrog and obtained the first generation of 1895 the following:

Dominating (Mephisto) 24%

Hybrids (with ±25% Danebrog) . 51%

⁸⁹ This is my translation of de Vries' text: "Cette loi n'est pas nouvelle. Elle a été énoncée, pour un cas particulier (les pois), il y a plus de trente années. C'est Gregor Mendel qui l'a formulé dans un mémoire intitulé « Versuche über Pflanzen-Hybriden », inséré dans le journal *Verhandlungen d. nat. Vereins in Brünn* (T IV, p. 1), 1865. Mendel en a déduit les conséquences non seulement pour les monohybrides, mais aussi pour les di-polyhybrides.

Ce mémoire, trop beau pour son temps, a été méconnu et oublié. On ne le trouve cité que rarement, et alors seulement pour des observations accessoires. Aussi n'en ai-je pris connaissance moi-même qu'après avoir achevé la partie la plus essentielle des expériences citées dans cet article, et notamment, après avoir trouvé la démonstration du principe par la quatrième année de culture (1896) de mes pavots croisés.

J'espère cependant avoir démontré que la loi de Mendel ne vaut pas seulement pour les pois, mais qu'elle s'applique d'une manière très générale à tous les vrais hybrides." (de Vries, 1900d, p. 271)

Recessive (Danebrog) 25%

This result is concordant with the formula cited above $[(d+r)(d+r)=d^2+2dr+r^2]$, or more correctly expressed, it was from these numerical relations that I first deduced the formula. (de Vries, 1966, p. 114)

From these numbers [25% (Const. Dom.) 50%(Hybrid) 25% (Const. Rec.)], I then first derived the law of segregation, while I did not yet know at that time the work of Mendel. (Kottler, 1979, p. 530)

According to de Vries' own accounts (de Vries, 1900a, 1900d, 1903), the experiment on *Papaver somniferum* began in 1893, and recognised 3 : 1 ratio and proposed the law of segregation in 1896. Thus, another puzzle occurs: why did de Vries not publish this discover immediately? As Malcolm Kottler asks, "[W]hy did de Vries wait until 1900 to publish, if he had obtained all the data and discovered their explanation (the laws) by 1896?" (Kottler, 1979, p. 530) Moreover, none of de Vries' pre-1900 papers even mentions such an interesting ratio in the hybrids of opium poppy. Nor is the 3 : 1 ratio of other hybrids mentioned.

According to his personal conversation to Ralph E. Cleland⁹⁰, de Vries' own explanation is that he was unsure about the universality of his explanation of the 3 : 1 ratio in 1896. Since he published the law of segregation in 1900, it is natural to infer that he was happy with the universality at that time. This inference seems to have been confirmed by de Vries' own statements. In his 1900 papers, de Vries emphasised that one major difference between his and Mendel's work is that Mendel only confirmed the law in pea hybrids, while he confirmed it in different plant hybrids.

These two statements [i.e. the law of segregation of hybrids], in their most essential points, were drawn up long ago by Mendel for a special case (peas). (de Vries, 1966, p. 110)

⁹⁰ "In a private conversation in 1928, de Vries told me that his failure to publish his findings prior to 1900 was because he obtained discordant results, *Oenothera* contrasting with the other plants he had studied; and he was endeavoring to understand more fully the reason for this discrepancy before publishing. His discovery in 1900 of Mendel's paper, however, stimulated him to begin the presentation of his results, and six papers appeared in that year." (Cleland, 1972, p. 10)

However, I wish that I had shown that Mendel's law not only is applied to peas, but also it is applicable to all true hybrids. (de Vries, 1900d, p. 271)

In two 1900 French papers, de Vries listed the results of the experiments on twelve different species to confirm the law of segregation. In the 1900 German paper, de Vries listed the data on sixteen species and the corresponding year of cross.⁹¹ All these data were also included⁹² in his book (1903).

Table 9

De Vries' important ratio published between 1897 and 1903						
	1897	1899		1900 German	1900m French	1903
<i>Lychnis vespertina</i> glabra × <i>Lychnis diurna</i> (began in 1892)	2/3 (hairy) : 1/3 (smooth)	99 (hairy) : 54 (smooth) 3/4 : 1/4				392 (hairy) : 144 (smooth)
<i>Lychnis vespertina</i> × <i>Lychnis glabra</i> (began in 1892)			72% (hairy) : 28% (smooth)	72% (hairy) : 28% (smooth)	72% (hairy) : 28% (smooth)	73% : 27%
<i>Lychnis diurna</i> × <i>Lychnis vespertina</i> (began in 1892)			73% (red) : 27% (white)	73% (red) : 27% (white)	73% (red) : 27% (white)	
<i>Papaver somnif.</i> <i>Mephisto</i> × <i>Danebrog</i> (began in 1893)			75% (black): 25% (white)	72% : 28%	75% : 25%	77.5% : 22.5% 158 (black) : 43 (white)
<i>Chrysanthemum</i>				77% :		80% : 20%

⁹¹ It is interesting to see the discrepancy between the German paper (de Vries, 1900a) and French papers (de Vries, 1900c, 1900d). I shall discuss it later.

⁹² Some were modified, see Table 9.

<i>Roxburghi</i> × <i>album</i> (began in 1896)				23%		
<i>Solanum nigrum</i> × <i>chlorocarpum</i> (began in 1894)				76% : 24%		77% : 73%
<i>Astertripolium</i> × <i>album</i> (began in 1897)				73% : 27%		75% : 25%

By analysing these data, I can summarise that by 1897 de Vries already had the results of nearly half of the crossing experiments (i.e. experiments on seven different species). In other words, as Kottler points out, it seems that de Vries “had established considerable generality.” (Kottler, 1979, p. 531) Again, it is puzzling why de Vries did not publish anything in 1897.

It is worth noting that in 1897, de Vries published a paper entitled “Erfelijke Monstrositeiten” in a Dutch journal, in which he recorded the result of an F2 generation of the cross of *Lychnis vespertina glabra* × *Lychnis diurna*: “the seedlings of 1894 were 2/3 pubescent [hairy] and 1/3 deprived of hair.” (Kottler, 1979, p. 519) Such a result was obviously not included in any of de Vries’ 1900 papers, since it is a 2 : 1 ratio rather than 3 : 1. But two years later, in a paper read the conference in London in July, 1899 de Vries seemed to modify the result into 3 : 1 implicitly.

If the white-flowering plants be isolated, it is found that they are fully constant. I fertilised them in 1893 in the first hybrid generation, when they were all hairy. The hairiness was inherited, as in the redflowered plants, in three-fourths of the individuals, but the white colour in nearly every individual. (de Vries, 1900b, p. 75)

Nevertheless, de Vries did not provide any explanation of the 3 : 1 ratio in that paper. What is more surprising, de Vries took this modified result as a piece of evidence for the law of segregation in his book (1903). If de Vries had established evidence for the law of segregation in 1897, he must have been

sensitive to the result of the cross of *Lychnis*. If so, why did he fail to see it as a piece of potential evidence? Thus, I suspect that it is likely that by 1897 de Vries had not recognised the 3 : 1 ratio. Even if he did, he still had not discovered the law, as Kottler (1979) argues. Furthermore, I am inclined to think that even in July 1899, de Vries still did not come to a “Mendelian” explanation.

De Vries’ Rediscovery and the 1896 Notes

However, in 1999 new evidence⁹³ was claimed to be found to support that de Vries knew the law of segregation independently in 1896. Stamhuis, Meijer and Zevenhuizen found notes dated 1896 in the Hugo de Vries Archive, in which contains the evidence of de Vries’ recognition of the 3 : 1 ratio and the law of segregation. In one of the sheets containing information on *Aster tripolium*, dated August 10, 1896, de Vries wrote:

Discussion. According to the law of pangene hybridization (p. 187), the purple specimens from white mother must have purple fathers and be central hybrids. They show therefore that the white specimens at Huizen (preferably almost entirely, partially? [inserted: 95%]) have been fertilized by purple ones. Just as my Trifol. pat. alb. have been fertilized by my 7-leaved race at 16b VI.

Therefore gain seed and sow it. If there are no white flowers this year and therefore all specimens are central hybrids, the seed must give 75% purples and 25% whites. This to be investigated.

At the same time this is a new principle in the transfer of varieties from the wild into the garden. If this happens after fertilization in the field, then all specimens from the seed can be look like old-types; then the variant will still emerge from their seed (namely in 25% of the specimens).⁹⁴ (Stamhuis, Meijer, & Zevenhuizen, 1999, pp. 249–250)

⁹³ This “new” evidence is in contrast to the Poppy Plate. Peter van der Pas (1976) and Jacob Heimans (1978) once accept that one of the lecture plates in the collection of the Museum of the University of Amsterdam on the cross of *Papaver somniferum* was used by de Vries in the lectures in 1895 and 1896. However, the belief that the Poppy Plate is a piece of evidence for that de Vries had discovered the law of segregation in 1896 was convincingly dismissed by Darden (1985) and Zevenhuizen (2000).

⁹⁴ The English translation quoted is from Stamhuis, Meijer and Zevenhuizen’s paper (1999).

In another note, dealing with *Veronica longifolia*, dated August 18, 1896, de Vries wrote:

According to the 1.2.1 law the old-types, no matter how they are pollinated, always give have to give 100% blue ones, while the central bastards in the case of free pollination (with the exception of whites), therefore by central bastards and by old-types, would have to give between 0 and 25% whites. (Stamhuis et al., 1999, p. 250)

At first glance, this discovery seems to be well consistent with de Vries' own claim that he first obtained the 3 : 1 ratio and the explanation in 1896. Both "the law of pangene hybridization" and "the 1.2.1 law" look so similar to the law of segregation, and easily make one to suspect them as the premature versions of the law of segregation. Based on these two notes, Stamhuis, Meijer and Zevenhuizen conclude that in 1896 de Vries already discovered the 3 : 1 ratio and the Mendelian explanation.

However, I find this conclusion unconvincing for the following reasons. Firstly, two species in the experiments noted are not included in de Vries' two French papers. If in 1896 de Vries had already recognised that the results from the crosses of *Aster tripolium* and *Veronica longifolia* are important to his law of segregation, why did not he include these results in his two 1900 French papers, especially the first one (de Vries, 1900c)? It seems that de Vries should not have forgotten these two important pieces of evidence. Secondly, the results of the crosses with these two species were included in de Vries' 1900 German paper and 1903 book. However there are discrepancies of the results, as shown in the Table 9. It is puzzling why de Vries made these changes. Thirdly, according to de Vries' 1900 German paper, *Aster tripolium* was crossed in 1897. So, de Vries should not have discussed the expected distribution of traits in the F₂ generation when the experiment was not undertaken. Fourthly, the terms "the law of pangene hybridisation" and "the 1.2.1 law" are so peculiar in de Vries' publications. It is still unclear what these laws exactly mean. Nor are these terms found in any of de Vries' publication. Therefore, I seriously doubt the originality of these two notes, and cannot regard them as evidence to

support that de Vries already noticed 3 : 1 ratio and formulated the law of segregation in 1896.

In addition, if one still remembers what was written in the letter to Roberts, it seems obvious that once again de Vries provides an inconsistent account. In the letter, de Vries implicitly reported that the 3 : 1 ratio was first recognised in 1895, one year earlier than the ratio was observed from the cross of *Papaver somniferum*. Whether this was accurate or not, I contend that this is another piece of evidence against de Vries' claim that he discovered the law of segregation from the cross of *Papaver somniferum* in 1896.

There is another conflict between de Vries' letter to Roberts and de Vries' 1900 German paper. According to the letter, de Vries began crossing *Oenothera lamarckiana* with *O. lam. brevistylis* in 1893. In contrast, in the German paper, de Vries recorded the year of crossing as 1898. (de Vries, 1966, p. 113) Hence, I believe that it is not hasty to conclude, at this moment, that most of de Vries' own accounts are inaccurate. In particular, as I have argued, de Vries' claim that he discovered the law of segregation from the cross of *Papaver somniferum* in 1896 is not well established.

Final Remarks on De Vries' Rediscovery

By carefully reading de Vries' publication from 1890s to 1903, I find that there are several substantial conceptual changes in 1900. Firstly, before 1900, no 3: 1 ratio nor 1: 2 : 1 ratio explicitly appeared in his publication. Secondly, in all his 1900 rediscovery papers, de Vries suddenly began using Mendel's term "dominant" and "recessive" to describe the morphological traits of the plant hybrids. It was de Vries' first 1900 paper (de Vries, 1900c), by using Mendel's terms, that made Correns to realise that de Vries also well knew Mendel's work, though without a reference to Mendel. Thirdly, before 1900, it seems that de Vries did not have the idea that the pair of characteristics can be separated and brought together again in new paired combination. All these conceptual changes indicate that there is some influence of Mendel's work on de Vries. Therefore, I now can conclude that de Vries' claim as to the independence of his rediscovery is ill grounded.

Correns' Rediscovery and the 1896 Protocol

The claim of Correns' independent rediscovery is not well established, either. Correns, according to his own narration, began conducting the experiment on *Pisum* in 1896.

I began (1894) with *Phaseolus vulgaris nanus* (with which, however, cross-fertilization did not succeed at all for me), then with *Zea*, *Pisum*, *Lilium* and *Matthiola*. (Roberts, 1929, p. 337)

In his letter to H. F. Roberts on January 23, 1925, Correns gives a detailed account of how he realised Mendel's priority.

The date of the day upon which in the autumn (October) of 1899, I found the explanation, I no longer know; I do not make note of such matters. I only know that it came to me at once 'like a flash,' as I lay toward morning awake in bed, and let the results again run through my head. Even as little do I know now the date upon which I read Mendel's memoir for the first time; it was at all events a few weeks later. (Roberts, 1929, p. 335)

The explanation mentioned in the letter was named "Mendel's rule"⁹⁵ (*Mendel'sche Regel*)" in Correns' paper (1900). However, this independence claim is dubious. According to Correns' other letter (on 30 January 1925) to Roberts, his original interest is the xenia question, and the experiments on *Pisum* are undertaken to investigate a similar question.

Originally I started out to solve the xenia question. To this end I wished to test experimentally all the assertions known in the literature. I began (1894) with *Phaseolus vulgaris nanus* (with which, however, cross-fertilization did not succeed at all for me), then with *Zea*, *Pisum*, *Lilium* and *Matthiola*... For *Pisum* there are different pertinent assumptions ... I had carried on cross-fertilizations with *Pisum* likewise on account of the xenia question (there exist, indeed, assumptions on the influence of the seed-coat)... (Roberts, 1929, p. 337)

⁹⁵ *Mendel'sche Regel* was translated by Piternick as "Mendel's law". However, *Regel* is better translated as "rule".

The xenia question, namely, whether foreign pollen has a direct influence on the characteristics of the fruit and seed, had puzzled many 19th century naturalists including Darwin for a long time. In order to study the xenia question, Correns planned to test all the known assertions in the literature. Conceivably, in order to study the problem in the case of *Pisum*, Correns must have also tried his best to survey the relevant literature. It would be a bit surprising if Correns, especially as a student of Nägeli, missed Mendel's paper. Hence, I am inclined to suspect that Correns must have known Mendel's paper before his experiment on *Pisum*, and the objective of his experiment on *Pisum* is to test Mendel's work.

This suspicion is not unfair. Correns' paper (1900) is easily seen as an attempt to examine Mendel's work on *Pisum*. This is well reflected from the title "G. Mendel's Law Concerning the Behaviour of Progeny of Varietal Hybrids" to the conclusion on the universality of "Mendel's rule". In particular, the paper contains the statements like:

The facts, which Mendel found, I can fully confirm. (Correns, 1900, p. 160, 1966, p. 122)

In order to explain the facts, one must assume (as did Mendel) that ...
(Correns, 1900, p. 163, 1966, p. 125)

... [T]hat Mendel's Law of segregation cannot be applied universally...
(Correns, 1900, p. 168, 1966, p. 132)

Correns' paper reads really like a report of the examination of Mendel's work on *Pisum*. This observation was also implicitly suggested by William Bateson (1902), who regarded Correns' paper as a report of a repetition of "Mendel's original experiment with Peas having seeds of different colours." If Correns had studied *Pisum* for a different purpose, or found a Mendelian explanation by himself independently, there may have alternative ways of writing his 1900 paper. However, it can be argued that by the time Correns wrote the paper, he had already known about Mendel's paper. My argument seems not to undermine Correns' independence claim in the sense that Correns did not know about Mendel's paper before his proposal of the Mendelian explanation.

Unfortunately, Correns' independence claim was falsified when Hans-Jörg Rieger (1995; 2000) found an entry written by Correns in his protocols of the experiment on peas (1896-1899) preserved in the Archive for the History of the History of the Max-Planck Society in Berlin. In this page carrying the date 16 August 1896, Correns clearly notes Mendel's analysis of the characters of peas with the reference to Mendel's paper (1865). (See Figure 5⁹⁶) Two conclusions can be drawn now. Firstly, my suspicion is confirmed. It is clear from this entry in 1896 that Correns was already attempting to analyse his experiment by following Mendel's approach. In particular, Correns noticeably adopted Mendel's terminology ("dominant"/ "recessive") to categorise the morphological traits, and thereof made a further analysis.

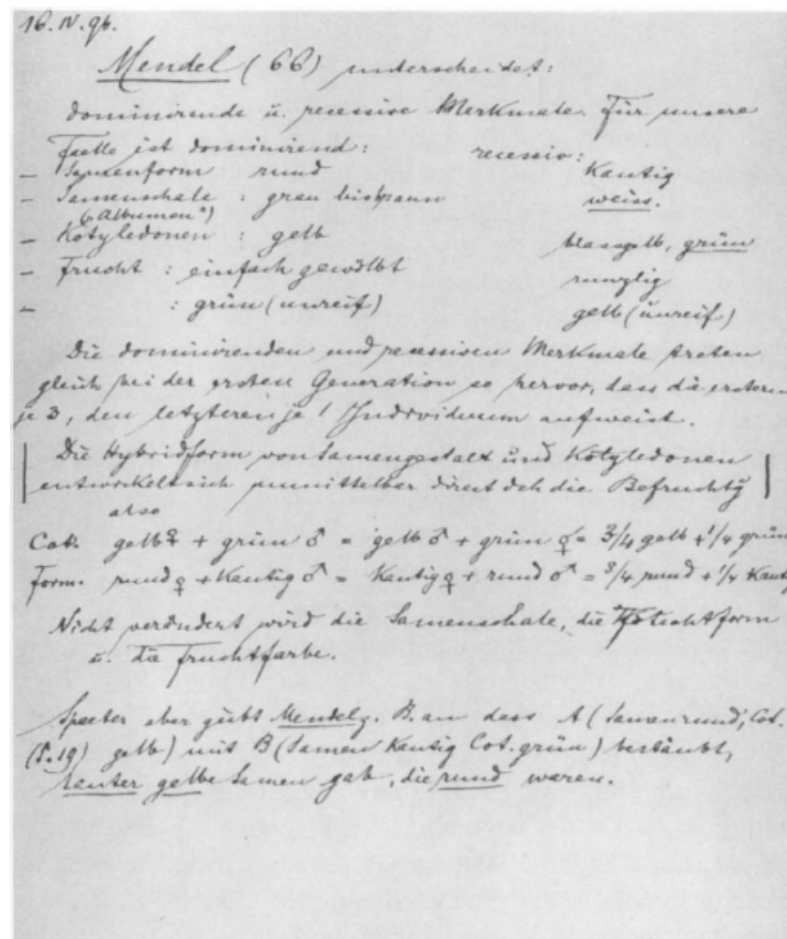


Figure 5

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Mendel (66) distinguishes:

⁹⁶ I acknowledge the permission to reprint this figure from the University of Chicago Press.

dominant and recessive characters. For our		
cases is	dominant:	recessive:
– form of seed	round	wrinkled
– seed coat: ("Albumen")	grey to brown	white
– cotyledons:	yellow	pale-yellow, green
– Pod:	inflated	constricted
– :	green (unripe)	yellow (unripe)

The dominant and recessive characters are expressed already in the first generation in such a way that the former are present in 3, the latter in 1 individual, respectively.

The hybrid form of seed shape and cotyledons develops immediately and directly through fertilization

Cot. (therefore) yellow? + green = yellows + green? = 3/4 yellow + 1/4 green Form.
round? + wrinkled = wrinkled? + rounds = 3/4 round + 1/4 wrinkled

The seed coat, the form and the colour of the pods are not changed.

But later Mendel notes, e.g., that A (seed round, Cot. (p. 19) yellow) pollinated with B (seed wrinkled Cot. green), exclusively yielded yellows seeds which were round.

(Hans-Jörg Rheinberger, 1995, pp. 613–614)

Secondly, if Correns, as stated in his letter to Roberts, did find a Mendelian explanation of the numerical relation in the progeny of pea hybrids in 1899, then he definitely had already read Mendel's paper. Therefore, it is sufficient to be concluded, as Rheinberger has suggested, that Correns must "have read Mendel's paper at the outset of his crossing experiments with peas, rather than after their completion." (Hans-Jörg Rheinberger, 1995, p. 614)

Tschermak's Rediscovery of the 3 : 1 Ratio?

The claim of Tschermak to have discovered Mendel's work independently is of the most dubious, and seems never to be well accepted⁹⁷. According to his own narration in a letter to Roberts in 1925, it was in the fall of 1899 that Tschermak first knew and read Mendel's paper (1865).

In the autumn of 1899, I received from Prof. A. v. Liebenberg the permission to volunteer in his department, and to make use of the library. The first work I seized upon was the well-known book of Focke: 'Pflanzenmischlinge,' of 1881. There I found, in the chapter on 'Peas,' the familiar obscure expression of Focke's concerning Mendel's treatise, as well as the views on Mendel's experiments with beans and Hieraceae. Since Mendel's work was not on hand in the library of the Hochschule für Bodenkultur, I had on the same day of this 'discovery' the 'Transactions of the Natural History Society of Brünn,' hunted out of the University library, which now gave me the information, to my greatest surprise, that the regular relationships discovered by me, had already been discovered by Mendel much earlier. Still, I believed myself to be at this time the only one who had made this discovery anew. (Roberts, 1929, p. 346)

In the same letter, Tschermak also confirms that his first reading of Mendel happened just shortly after his discovery of the 3:1 ratio from the results of his experiment on peas, which began in the spring of 1898. (Roberts, 1929, pp. 343–345) This account is consistent with his retrospective view in a lecture in 1950.

In studying the results of my pea crosses in the fall of 1899 I discovered the 3:1 segregation ratio for yellow and green cotyledons and smooth and wrinkled seeds, as well as the 1:1 ratio in backcrossing the green cotyledon peas with hybrid pollen, in the second seed generation of all of my experimental groups.

While recording these results I saw the citation of Mendel in Focke's book and obtained from the University library the volume of the *Naturforschender Verein in Brünn* containing Mendel's paper. There I read to

⁹⁷ Stern and Sherwood did not even include von Tschermak's paper in their anthology *The Origins of Genetics, A Mendel Source Book* for the reason that his study "had fallen short of the essential discovery." (C. Stern & Sherwood, 1966, pp. xi–xii)

my great surprise that Mendel had already carried out such experiments much more extensive than mine, had noted the same regularities, and had already given the explanation for the 3:1 segregation ratio. This was the first surprise I encountered in the preparation of my *Habilitationsschrift* which I hurried to completion in order to hand it to the editors of our Institute on January 17th, 1900. (Tschermak, 1951, p. 169)

To sum up, Tschermak claims that he learnt of Mendel and his paper from Focke's book and his first reading of Mendel's paper happened after his discovery of the regularity found in the results of the experiment on peas. However, two points should be noted. Firstly, in both accounts, what really surprised Tschermak when he first read Mendel's paper is that Mendel already discovered "the regular relationships" he discovered. In contrast, he did not emphasise that Mendel's explanation of 3:1 ratio is the same as his if he really had one mind at that time. It would be really surprising if Tschermak forgot to mention such a coincidence. As we have seen from de Vries' and Correns' statements, both of them emphasised that their first reading of Mendel's paper (1865) was after their proposal of the Mendelian law. Thus, I suggest that Tschermak did not have a Mendelian explanation before his first reading of Mendel's paper.⁹⁸

Secondly, Tschermak's claim that he recognised the 1 : 1 ratio in the results of backcrossing in 1899 is not supported by his paper (1900b). Though he recorded the results of back-crossing, the 1 : 1 ratio was not explicitly stated.

When fertilized by the parental type with the recessive character, the number of bearers of the recessive character are increased over that of self-fertilization of the hybrid. The influence of the character "yellow" in the seeds in the hybrid was in this case reduced by 57 per cent, while that of the character "green" was reduced by 43.5 percent. (Tschermak, 1900b, p. 237, 1950, p. 46)

⁹⁸ In fact Tschermak did not provide any explanation of the 3 : 1 ratio in his papers (1900a, 1900b) at all! Nor is any lawlike statement explicitly made. See more discussion on this in the section 4.2.

It is far from clear that 57% : 43.5% is identical with the 1 : 1 ratio. Hence, I argue that Tschermak could not have recognised the 1 : 1 ratio in the results of backcrossing in 1900.

As shown in Table 7, in 1900 Tschermak published two “rediscovery” papers with the same title “Über künstliche Kreuzung bei *Pisum sativum*”. The short one (Tschermak, 1900b) was published in June 29th in the same Journal where de Vries’ and Correns’ papers were published in March and April respectively, while the longer one (Tschermak, 1900a) was published in *Zeitschrift für das landwirtschaftliche Versuchswesen in Oesterreich* a few months later. According to Tschermak’s own accounts (Roberts, 1929; Tschermak, 1951), the long version was prepared much earlier and was submitted on January 17th, 1900, though he also made some corrections by checking de Vries’ paper (de Vries, 1900c) and Correns’ paper (1900).

By Christmas, my paper was finished, ready for publication, and on the 17th of January... In the meantime there appeared soon thereafter the extensive work of De Vries in the Reports of the German Botanical Society (Heft 3). I was able to utilize it already as early as during the correction of my proofs. On the reading of the second proof I was surprised anew by the work of Correns (Ber. d. d. Bot. Gesell. Heft 4, April 24). I was therefore able to take it into consideration only in the footnote to my first paper. As may readily be conceived, I now made every effort to induce the publisher of the journal before-mentioned, as well as the printing office, to publish the separates of my work before the appearance of the number in question, which, fortunately, likewise succeeded (May, 1900). In the meantime, I wrote quickly an abstract of my paper, for the Berichte der deutschen botanischen Gesellschaft (received for publication June 2, Heft 6), which, however, appeared somewhat later than the separates of my complete paper, which I immediately sent out. (Roberts, 1929, p. 346)

As seen in the quote above, Tschermak’s short paper (1900b), or “abstract” in his word, was written after the publication of Correns’ paper. So it can be inferred that the abstract was written in May 1900. Thus, it is quite certain that Tschermak’s first reading of Mendel’s paper happened earlier than his completion of the paper, and

much earlier than the beginning of his writing of the abstract. This conclusion is further confirmed by new evidence uncovered recently. Michal Smunek, Uwe Hoßfeld, and Olaf Breidbach found in a letter dated April 4th, 1900, Tschermak had been commented that he well understood Mendel at that time by his brother, Armin von Tschermak.

But [de Vries] doesn't know the teaching of Mendel! Ha! Ha! But please don't offend him: He will need to learn it from you! (Simunek, Hoßfeld, & Breidbach, 2011, p. 838)

Twelve days later, Armin Tschermak suggested his brother to write an abstract of the long paper (Tschermak, 1900a) for publication. So it can be inferred that Tschermak's abstract (1900b) was written after 16 May 1900. If so, the correspondence between Tschermak brothers, though indirectly, shows that before writing the abstract, Tschermak had made a careful reading of Mendel's paper, as well as de Vries' (de Vries, 1900a) and Correns' (1900).

Moreover, it is dubious if Tschermak independently recognized the 3 : 1 ratio. It is not obvious for a reader by reading Tschermak's long paper (1900a) to see that he had recognised the 3 : 1 ratio before his first reading of Mendel and regarded it as a new discovery. In order to show his independence of the discovery of the 3 : 1 ratio, Tschermak, in his letter to Roberts (1929), claims that he initially conceptualized the 3 : 1 ratio in a different way as Mendel did.

[In the paper (Tschermak, 1900a)] I emphasized besides that instead of 'dominieren' [dominate], one should say rather 'prävalieren' [predominate], at least in certain cases... (Roberts, 1929, p. 345)

If this were the case, Tschermak's initial formulation of the 3 : 1 ratio in terms of predominance (*prävalieren*) was a good piece of evidence to support the independence. Unfortunately, as I shall show in the next section, Tschermak's non-Mendelian conceptualization of the 3 : 1 ratio was not very sophisticated until his 1901 papers. In particular, Tschermak (1900a, 1900b) did not have a counterpart concept compared to Mendel's "recessiveness". It is not convincing that Tschermak recognised the 3 : 1 ratio in terms of predominance initially before

reading Mendel's paper. Therefore, Tschermak's independence of the rediscovery is undermined.

4.2 “Rediscovery”: A Misleading Characterisation

Another line of criticism on the rediscovery thesis is to challenge the conventional usage of the term “rediscovery” to designate the publication of de Vries, Correns, and Tschermak’s papers in 1900 and its impact.⁹⁹ When talking of “the rediscovery”, one may easily have the impression that de Vries, Correns, and Tschermak’s contribution is merely a re-introduction of Mendel’s work. However, the real story is much more complicated. As we shall see, de Vries, Correns, and Tschermak were studying different problems, all of which are different from Mendel’s concern. In the rediscovery papers, they painstakingly conceptualised the results of their experiments by adopting Mendel’s approach within their own theoretical frameworks. As Orel points out, “there was a process of incorporation of Mendel’s innovative [work]¹⁰⁰.” (Orel, 1996, p. 289) So it is not legitimate to call what de Vries, Correns, and von Tschermak did around 1900 the rediscovery. In this section I shall develop and strengthen Orel’s view to show the incorporation is a better term to characterise and reflect the contribution of de Vries, Correns, and Tschermak in 1900 by making an in-depth analysis of their conceptual frameworks.

Tschermak’s “Rediscovery”: The 3 : 1 Ratio and the Valency of the Trait

In order to evaluate whether the term “rediscovery” correctly captures de Vries’, Correns’ and Tschermak’s contribution to the history of genetics, I find it necessary to clarify what the “rediscovery” means. There are various phrases of the rediscovery story: “the rediscovery of Mendel’s work” (for example, Corcos & Monaghan, 1985; Iltis, 1932; Orel, 1996; R. G. Punnett, 1919), “the rediscovery of Mendelism” (for example, Harwood, 2000; C. Stern & Sherwood, 1966; Zirkle, 1968),

⁹⁹ It should not be confused with the criticism on the long-neglect thesis. The long-neglect thesis is sufficiently countered by the evidence of the references to Mendel in pre-1900 publications. However, the criticism I shall discuss and develop in this section is to argue that the actual practice of de Vries, Correns, and Tschermak is too complicated to be summarised by the term “rediscovery”. In other words, the term “rediscovery” oversimplifies the actual practice of de Vries, and Correns, and Tschermak in 1900.

¹⁰⁰ Orel’s original term used here is “ideas”. However I find that the term “ideas” connotes a limited aspect of Mendel’s contribution. In fact, as I shall show later, Mendel’s influence on de Vries, Correns, and Tschermak is in many ways. As Orel himself well recognizes, “After reading Mendel’s paper [de Vries, Correns, and Tschermak] definitely revised the methods used in their further experiments, and above all interpreted the results taking into account Mendel’s approach to research in plant hybridization so far as they had perceived it.” (Orel, 1996, p. 289) Hence, I employ the term “work” to embrace Mendel’s theoretical and practical contribution.

and “the rediscovery of Mendel’s law(s)” (for example, Bateson, 1902; Bowler, 1989; Kottler, 1979; Simunek et al., 2011; Stubbe, 1972). In fact all these phrases are used interchangeably (for example, Corcos & Monaghan, 1985, 1987a, 1987b; Monaghan & Corcos, 1986, 1987; Tschermak, 1951). Conventionally, both Mendel’s work and Mendelism are identical with Mendel’s law of inheritance. However, as I have argued in Chapter 3, Mendel’s laws are in fact not about inheritance and cannot be understood as laws of inheritance, so it is obviously illegitimate to name the rediscoverers’ publications in 1900 the rediscovery of Mendel’s laws. Nevertheless, it is still worth investigating what de Vries, Correns, and Tschermak in fact “rediscovered” respectively, and what is a best way to understand these activities.

Let me begin with Tschermak. As I have mentioned, Tschermak, according to his narration in the first 1900 paper (1900b), began his hybridisation experiment on *Pisum sativum* in 1898. He focused on observing the inheritance patterns of two pair of morphological traits, namely, yellow/green storage tissues and round/wrinkled seeds. In order to analyse the results, Tschermak followed Mendel to designate “dominant” characters to yellowness and roundness and “recessive” to greenness and wrinkleness. In the F₂ generation, Tschermak recognised the 3 : 1 ratio between dominant and recessive characters.

The ratio of seeds carrying the dominant, prevailing character to those carrying the recessive is about 3 : 1. (Tschermak, 1900b, p. 236, 1950, p. 45)

In the long paper (Tschermak, 1900a, p. 536), Tschermak reports the ratio in greater details as follows.

Yellow-seeded	Green-seeded	
1854	660	= 2.8 : 1
Smooth-seeded	Wrinkled-seeded	
884	288	= 3.1 : 1

However, Tschermak did not provide any “deeper” explanation of the 3 : 1 ratio at all! Nor does he deduce any “Mendel’s rule” or “the law of segregation” explicitly, unlike de Vries and Correns did. In the postscript of his papers (Tschermak, 1900a,

1900b), Tschermak enunciates that he believed that he “had found something new”, and his hybridisation experiment and observation “confirm Mendel’s teaching”, but he nowhere explicitly tells us what Mendel’s teaching is in the paper. All I can justifiably infer from Tschermak’s paper (1900b) is that if there is a new thing he believed that he found, it only can be the 3 : 1 ratio. It is also confirmed by Tschermak’s own retrospect fifty years later.

In studying the results of my pea crosses in the fall of 1899 I discovered the 3:1 segregation ratio for yellow and green cotyledons and smooth and wrinkled seeds, as well as the 1:1 ratio in backcrossing the green cotyledon peas with hybrid pollen, in the second seed generation of all of my experimental groups.

While recording these results I saw the citation of Mendel in Focke's book and obtained from the University library the volume of the *Naturforschender Verein in Brünn* containing Mendel's paper. There I read to my great surprise that Mendel had already carried out such experiments much more extensive than mine, had noted the same regularities, and had already given the explanation for the 3:1 segregation ratio. (Tschermak, 1951, p. 169)

It is quite clear that even Tschermak himself identified what he rediscovered is the 3 : 1 ratio. It is a rediscovery if he did recognise the ratio!¹⁰¹ On the one hand, it is not an easy task to obtain such a ratio in the crossing independently for a nineteenth century experimenter. As Zirkle puts it, “To recognize a Mendelian ratio for the first time requires a certain amount of plain good luck.” (Zirkle, 1968, p. 214) On the other hand, it is really difficult to recognise the 3 : 1 ratio by idealising the raw data if one does not have a Mendelian explanation on mind. As shown in the crossing between *Lychnis vespertina glabra* and *Lychnis diurna*, de Vries initially only saw the 2 : 1 ratio in the F₂ generation in 1897 and did not recognise that it was the 3 : 1 ratio until his reading of Mendel’s paper.

¹⁰¹ However, I am still sceptical on if Tschermak realised the significance of the 3 : 1 ratio in 1899. The 3 : 1 ratio (or more specifically the 1 : 2 : 1 ratio) was important for Mendel because it could be well explained by his law of development concerning a pair of traits. But for Tschermak, even if he recognised the 3 : 1 ratio independently, the ratio itself, as a mere description of the phenomenon, seemed hardly an important discovery if it yielded no theoretical or practical implications.

However, it is obvious that Tschermak did not conceptualise the ratio in the way as Mendel did. Mendel and Tschermak had different concerns. As I have emphasised in the Chapter 3, Mendel's concern is about the development of hybrids. In contrast, Tschermak's main purpose is to study the influence (*Einfluss*) of foreign pollen on the morphological traits by observing the inheritance (*Vererbung*) of the constant morphological traits.

The purpose was to study the immediate influence of the foreign pollen upon the constitution (form and color) of the seeds thus produced, and also to follow, in the next generation of hybrids, the inheritance of the constant, differentiating characters of the parental types used in the hybridization. (Tschermak, 1900b, p. 232, 1950, p. 42)

Moreover, Mendel's law is noticeably called the "principle of the regular non-equivalence of characters"¹⁰² (*Satz von der gesetzmässigen Ungleichwerthigkeit der Merkmale für die Vererbung*) by Tschermak (1900a, 1900b).

The principle, established by [Mendel], of the regular non-equivalence of characters in inheritance [*der gesetzmässigen Ungleichwerthigkeit der Merkmale für die Vererbung*], is confirmed by my experiments on *Pisum sativum*. Likewise the observations of Körnicke, Correns and de Vries on *Zea Mays* as well as those made by de Vries in his species crosses, completely corroborate it. It proves to be of the highest significance for the study of inheritance in general. (Tschermak, 1900b, p. 235, 1950, p. 44)

It should be emphasised as a special merit of [Mendel] that he discovered the principle of the regular non-equivalence of characters in inheritance and clearly proved it in the most suitable species *Pisum sativum*.¹⁰³ (Tschermak, 1900a, p. 513)

¹⁰² This is Hannah's translation (Tschermak, 1950, p. 44).

¹⁰³ This is my translation of Tschermak's text: "Es muss als besonderes Verdienst dieses Beobachters hervorgehoben werden, dass er die gesetzmässig ungleiche Werthigkeit der verschiedenen Merkmale für die Vererbung erkannte und an der besonders geeigneten Species *Pisum sativum* klar erwies." (Tschermak, 1900a, p. 513)

According to my summary in the section 3.2, there is no such a law named “the principle of the regular non-equivalence of characters” in Mendel’s paper (1865). Though Tschermak did not explicitly formulate this principle or define the term valency (*Werthigkeit*) in his paper (1900a, 1900b), his terminology did sufficiently reflect that he tried to reformulate Mendel’s law within a different conceptual framework. As the new name suggests, Tschermak reformulates Mendel’s law in terms of the valency of the trait (*die Werthigkeit der Merkmale*). In his paper (1901c), Tschermak explicated Mendel’s law, which is renamed “Mendel’s principle of regular differential valency¹⁰⁴ of traits in heredity” (*MENDEL’schen Lehre von der gesetzmässigen Verschiedenwerthigkeit der Merkmale für die Vererbung*)¹⁰⁵. For Tschermak (1901c), Mendel’s principle consists of three principles: the principle of regular dimensional valency of traits (*der Satz von der gesetzmässigen Masswerthigkeit der Merkmale*), the principle of regular quantitative valency of traits (*der Satz von der gesetzmässigen Mengenwerthigkeit der Merkmale*), and the principle of regular hereditary valency of traits or the principle of segregation of traits (*der Satz von der gesetzmässigen Vererbungswerthigkeit oder Spaltung der Merkmale*).

The principle of regular dimensional valency of traits states that certain traits change their form in the hybrids. The principle of regular quantitative valency of traits states that the number of carriers¹⁰⁶ of the dominant trait and of the recessive traits is in a constant ratio in each generation. The principle of regular hereditary valency of traits or the principle of segregation of traits states that the ratio of the dominant trait to the recessive one is 3 : 1. For Tschermak (1900a, p. 532), the valency of the trait is referred to the influence (*Einfluss*) of the trait to prevail in the subsequent generations.

¹⁰⁴ Simunek, Hoßfeld, and Wissemann (2011; 2012) translate *Wertigkeit* as value or valuation. In contrast, along with Olby (1985, 1987), I find “valency” is a better translation.

¹⁰⁵ Though the slight difference of the names, considering the similar meaning of *Ungleich* and *Verschiede*, I argue that both *Satz von der gesetzmässigen Ungleichwerthigkeit der Merkmale für die Vererbung* and *MENDEL’schen Lehre von der gesetzmässigen Verschiedenwerthigkeit der Merkmale für die Vererbung* refer to Mendel’s laws (1865).

¹⁰⁶ The term carrier (*Träger*) here should be not understood as a counterpart concept compared to Correns’ concept *Anlage*, or the later concept gene. Rather Tschermak here refers the number of carriers of dominating character to the number of plants with dominating character. Thus, I agree with Olby (1985, p. 123) that Tschermak “had not arrived at” the conception of germinal segregation.

By his examination, Tschermak (1900a, p. 555, 1900b, p. 239) admits, along with Correns, that Mendel's law is not universally applicable, but he (1901c, p. 51) still insists that "Mendel's law" is a classical teaching (*klassische Lehre*) for its significance in the theory and practice of plant breeding.

Although Tschermak's understanding of Mendel's law in terms of valency of trait in 1900 was not as sophisticated as his in 1901, it is beyond doubt that he began analysing and understanding the experiments in a similar way where he mostly talked of the influence of the trait.

The taller type always has the greater influence, regardless of whether it characterized the maternal or paternal variety. (Tschermak, 1900b, p. 234, 1950, p. 44)

Certain specific combinations yielded this effect with regularity. The characters which were taken into consideration to recognize such an influence, related to the form of the seeds and the color of the storage tissue. (Tschermak, 1900b, pp. 234–235, 1950, p. 44)

The influence of the character "yellow" in the seeds in the hybrid was in this case reduced by 57 per cent, while that of the character "green" was reduced by 43.5 percent. (Tschermak, 1900b, p. 237, 1950, p. 46)

As to the relative influence (or the relative valency) of parental plants on the height, my experiments draw the following conclusions ...¹⁰⁷ (Tschermak, 1900a, p. 532)

Moreover, in his publications between 1900 and 1901 (1900a, 1900b, 1901a, 1901b), the valency of the trait was definitely a key word. In other words, Tschermak's research during this period was conceptualised in terms of the valency of the trait. Thus, it is reasonable to conclude that Tschermak's papers (Tschermak, 1900a, 1900b) contained his premature attempts to analyse the 3 : 1 ratio in terms of valency of traits in heredity.

¹⁰⁷ "Bezüglich des relativen Einflusses (oder der relativen Werthigkeit) eines verschiedenen Höhenmerkmals der Vater- und der Muttersorte gestatten meine Versuche folgende Schlüsse: ..." (Tschermak, 1900a, p. 532)

Now it is the time to reassess Tschermak's contribution in 1900. Stern once remarkably rejected Tschermak as a rediscoverer by arguing that "[Tschermak's] publications in 1900 show him... only an experimenter whose understanding... had 'fallen short of the essential discovery'." (C. Stern & Sherwood, 1966, pp. xi–xii) Stern is both right and wrong. He is right on the point that Tschermak's publications in 1900 cannot be regarded as a rediscovery of Mendel's theoretical work. It is a fair point that, despite recognising the 3 : 1 ratio, Tschermak showed an insufficient understanding of Mendel's paper in his papers (Tschermak, 1900a, 1900b). Nor is the significance of the 3 : 1 ratio was highlighted or explored adequately by Tschermak in 1900. On the other hand, Stern is wrong. Tschermak was more than an experimenter: He was also a theorist attempting to conceptualise the 3 : 1 ratio in terms of the valency of traits and to adopt Mendel's analysis to develop his own theory. In short, it is better to understand Tschermak's practice in 1900 as an incorporation of Mendel's approach into his analysis of valency of traits in heredity rather than a rediscovery of Mendel's work.

Correns' "Rediscovery": Testing and Reformulating Mendel's Work

Unlike Tschermak, Correns was very explicit, in his paper (Correns, 1900), on the point that what he rediscovered is "the regularity of the phenomena, and the explanation thereof". Furthermore, after citing Mendel's law of composition of hybrid fertilising cells (LCC), Correns explicitly reformulated it as an explanan:

In the hybrids form, reproductive cells are produced in which the anlagen for the individual parental characteristics are contained in all possible combinations, but both anlagen for the same pair of traits are never combined. Each combination occurs with approximately the same frequency. (Correns, 1900, p. 166, 1966, p. 130)

Correns believed that he found the "exactly same explanation" as Mendel and de Vries did for the regular ratio obtained from the progeny of hybrids. However, such a claim is problematic. There are substantial conceptual differences between Correns' "Mendel's rule" (*Mendel's Regel*) and Mendel's laws. A first obvious difference is about terminology. While both Mendel (1865) and de Vries (1900a) used the term *Gesetz* (law), Correns cautiously employed the term *Regel* (rule). It is

not surprising, since Correns repeatedly emphasised the limited applicability of Mendel's rule¹⁰⁸ in the paper (Correns, 1900).

At present, however, this [rule] is applicable only to a certain number of cases... It seems impossible that all pairs of characters of all hybrids should behave according to this [rule]. (Correns, 1900, p. 167, 1966, p. 131)

... [T]hat Mendel's [rule] of segregation cannot be applied universally. (Correns, 1900, p. 168, 1966, p. 132)

On the other hand, Mendel was a bit more confident, though he still was uncertain on the generality of his laws.

Yet even the validity of the laws [Sätze] proposed for *Pisum* needs confirmation, and a repetition of at least the more important experiments is therefore desirable... Whether variable hybrids of other plant species show complete agreement in behavior also remains to be decided experimentally; one might assume, however, that no basic difference could exist in important matters since *unity* in the plan of development of organic life is beyond doubt. (Mendel, 1865, pp. 42–43, 1966a, p. 43)

This difference is more than a linguistic issue. Rather it reflects a difference of the views on the applicability of the “law” between Correns, and Mendel.

A second significant difference between Correns' and Mendel's work is that Mendel conceptualised LCC in terms of kinds of cells (*die Arten von Zellen*), while Correns in terms of anlagen (*Anlagen*) in the cell. The anlagen here follows August Weismann's usage (1892) to name the primary constituents in the germ cell. Correns refined it to implicitly designate the hereditary material for a morphological trait in the nuclei and the unit of segregation during the formation of the reproductive nuclei.

... [P]rior to the definitive formation of the reproductive nuclei a complete separation of the two anlagen occurs, so that one half of the reproductive

¹⁰⁸ In order to emphasise the difference, in the following I shall use the term “Mendel's rule” as the translation of Corren's “*Mendel's Regel*”. In other cases, I shall use the term “Mendelian Rule” to refer to Correns' “*Mendel's Regel*”.

nuclei receive the anlage for [one trait], the other half the [other]. (Correns, 1900, p. 166, 1966, p. 126)

As Correns himself points out in the footnote (1900, p. 163 n1), Mendel did not mention nuclei in his paper. Nor did Mendel talk of the fusion of the reproductive cells, or anlagen. It is obvious that cells and anlagen are in the different biological level. Anlagen, for Correns, are hereditary material in the nuclei of cells. Again, this reformulation is not just about terminology. It is a good example of what Olby calls an extension of “the explanatory level of [Mendel’s] paper on the basis of [the rediscoverers’] own understanding of the recent developments in cytology”. (Olby, 1985, p. 242) Furthermore, Correns implicitly suggests that a pair of traits is determined by a pair of anlagen, while Mendel, as Olby (1979, 1985) suggests, never had such an idea of “the quantitative equivalence” between traits and kinds of cells. Mendel did postulate that kinds of cells correspond to the morphological traits, but he was not very clear on the numerical relation of kinds of cells and traits. Thus, the shift from kinds of cells to anlagen is a significant conceptual change beyond Mendel made by Correns.

Thirdly, Correns differs from Mendel in using the terms “dominating” and “recessive”. Mendel uses the terms “dominating/recessive”, especially the term “dominating” in two ways. On the one hand, “dominating” refers to a parental trait, which would dominate in the hybrid. On the other hand, “dominating” refers to a hybrid trait with a certain behaviour in its progeny (i.e. in all its progeny the trait would exhibit the same pattern as in the first generation). Although Correns also employs the terms “dominating” and “recessive” in two ways, his usage is slightly different. The terms are attributed to both morphological traits and anlagen.

In many pairs one trait, or rather the anlage thereof, is so much stronger than the other trait, or its anlage, that the former alone appears in the hybrid plant, while the latter does not show up at all. This one may be called dominating, the other one the recessive, ... (Correns, 1900, p. 159, 1966, p. 121)

Another point should also be highlighted. Correns’ Mendelian Rule is more than a reformulation of Mendel’s law of composition of hybrid fertilizing cells (LCC) in

terms of anlagen. Correns' formulated version of LCC is only one constituent of "Mendel's rule". The other constituent is quoted as follows.

If the parental strains differ only in one pair of traits (2 traits: A, a) the hybrid will form only two types of reproductive nuclei (A, a) which are like those of the parents. Each type is 50 percent of the total. If the parents differ in two pairs of traits (4 traits: A, a; B, b) four types of reproductive nuclei will be formed, (AB, Ab, aB, ab) and 25 percent of the total will be of each type. If the parents differ in three pairs of traits (6 traits: A, a; B, b; C, c) eight types of reproductive nuclei will be formed (ABC, ABc, AbC, Abc, aBC, aBc, abC, abc), and 12.5 percent of the total are of each type. (Correns, 1900, p. 166, 1966, pp. 130–131)

This formulation clearly involves the ideas from both Mendel's LCC and LCT. Hence, Correns' Mendelian Rule is definitely not just a reformulation of Mendel's law. Correspondingly, Correns' contribution cannot be simply construed as a confirmation of Mendel's laws or a re-introduction and reformulation of Mendel's laws in terms of anlage.

As I have already argued, Correns' original purpose of his experiments on *Pisum* was to test all the relevant assertions in the literature. This purpose is well reflected in Correns' paper (1900) from the title "G. Mendel's Law Concerning the Behaviour of Progeny of Varietal Hybrids" to the conclusion on the universality of "Mendel's rule". The paper is easily seen as an attempt to examine Mendel's work, which contains the statements like:

The facts, which Mendel found, I can fully confirm. (Correns, 1900, p. 160, 1966, p. 122)

In order to explain the facts, one must assume (as did Mendel) that ... (Correns, 1900, p. 163, 1966, p. 125)

... [T]hat Mendel's Law of segregation cannot be applied universally... (Correns, 1900, p. 168, 1966, p. 132)

Thus, it is very clear that the objective of Correns' paper is to test Mendel's work on *Pisum*. This observation was also implicitly suggested by William Bateson (1902), who regarded Correns' paper as a report of a repetition of "Mendel's original experiment with Peas having seeds of different colours." If Correns had studied *Pisum* for a different purpose, or found a Mendelian explanation by himself independently, there may have been alternative ways of writing his 1900 paper. Moreover, as I have shown, the entry Rheiberger found (Figure 5) can also be construed as a piece of evidence to support that Correns' concern is to test Mendel's work on *Pisum*. Thus, now I contend that it is quite well established that Correns' experiment on *Pisum* originates from his project of testing Mendel's work. However, Correns' paper finally turned out to be more than a mere confirmation of Mendel's work. It also provides a new analysis of the behavior of the progeny of *Pisum* by incorporating Mendel's and Weismann's work. Therefore, Correns' work cannot be simply summarised as a rediscovery.

de Vries' "Rediscovery": The Law of Segregation as the Evidential Support of Theory of Pangenesis

In his 1900 papers, de Vries claimed that what he rediscovered is "the law of segregation".

The totality of these experiments establishes the law of segregation of hybrids... (de Vries, 1900c, p. 847, 1950, p. 32)

From these and numerous other experiments I draw the conclusion that the law of segregation of hybrids as discovered by Mendel for peas finds very general application in the plant kingdom... (de Vries, 1900a, p. 84, 1966, p. 117)

The law of segregation¹⁰⁹ is explicitly formulated by de Vries as follows.

¹⁰⁹ It should be noted that de Vries' law of segregation is only confirmed by the crossing experiments on plants with the antagonistic characteristics, as he explicitly claims, "The crossing experiment is thereby limited to the antagonistic characteristics." (de Vries, 1966, p. 110) In other words, even if as de Vries contends that the law of segregation has a "general application in the plant kingdom", it is still only applicable to a limited class of hybrids (i.e. those with antagonistic characteristics).

The pollen grains and ovules of monohybrids are not hybrids but belong exclusively to one or the other of the two parental types. (de Vries, 1900a, p. 86, 1966, p. 112)

At first glance, it seems evident that this is hardly a rediscovery, since Mendel never made such a statement or a similar statement. Moreover, none of Mendel's three laws can be simply identified with an early version of de Vries' law of segregation. Mendel's laws are either about the numerical relationship between the traits of the hybrid and its progeny, or about the correspondence between the combination of traits and the composition of cells, while de Vries' law of segregation is literally about the behaviour of the pollen grains and ovules in the generative period. In other words, Mendel did not have a law of segregation in de Vries' sense. Nor did Mendel even use the term segregation (*Spaltung*). It is de Vries' contribution to coin the term "law of segregation (*Spaltungsgesetz*)" and to designate it to a phenomenon in the formation of pollen and ovules.

Some might argue that de Vries' law of segregation is derived from the analysis of his hybrid experiments with a Mendelian approach (e.g. the usage of the concepts "dominating/recessive" and the recognition of the 3:1 ratio), so it is still plausible to defend the view that de Vries' work can be understood as a rediscovery of Mendel's work in a broad sense. However, I shall argue that the Mendelian elements in de Vries' work well reflect an incorporation rather than a rediscovery.

First of all, de Vries regards the law of segregation as a piece of evidence for his own theory. As I have argued, Mendel's work on hybrids was to study the development of hybrid and its progeny. However, de Vries had a different concern. His work on hybrids was to defend his theory of heredity: the theory of pangenesis (1889). This purpose was clearly stated in the introductions of de Vries' papers (1900a, 1900c).

According to the principles which I have expressed elsewhere (Intracelluläre Pangenesis, 1889), the specific characters of organisms are composed of separate units. One is able to study, experimentally, these units either by the phenomena of variability and mutability or by the product of hybrids. (de Vries, 1900c, p. 845, 1950, p. 30)

According to pangenesis the total character of a plant is built up of distinct units... For many years this principle has represented the starting point for my investigations. Many important consequences can be deduced from it and may be tested experimentally. My experiments lie in part in the realm of variability and mutability and in part in that of hybridization. (de Vries, 1900a, p. 83, 1966, p. 107)

Thus, de Vries' finding of the law of segregation originates from his study of hybridisation to test the theory of pangenesis experimentally. Moreover, in the conclusions, de Vries contends that his law of segregation confirms the theory of pangenesis.

The totality of these experiments establishes the law of segregation of hybrids and confirms the principles that I have expressed concerning the specific characters considered as being distinct units. (de Vries, 1900c, p. 847, 1950, p. 32)

From these and numerous other experiments I draw the conclusion that the law of segregation as discovered by Mendel for peas finds very general application in the plant kingdom and that it has a basic significance for the study of the units of which the species character is composed. (de Vries, 1900a, p. 84, 1966, p. 117)

For de Vries, the law of segregation was important because it seemed to support the theory of pangenesis in 1900. Thus, de Vries' finding of the law of segregation is better characterised as a confirmation of his theory of pangenesis rather than a rediscovery of Mendel's work.

Secondly, de Vries' usage of the term "dominant/recessive" (1900a, 1900c, 1900d) was an incorporation of Mendel's (1865) and his old terminology (1889) rather than a rediscovery of Mendel's usage. It was noticeable that de Vries interchangeably used the term "dominant" with "active (or visible)" on the one hand, and "recessive" with "latent" on the other hand in his 1900 papers.

In the hybrid the simple differential character from one of the parents is accordingly visible or dominant while the antagonistic character is in the latent condition or recessive.¹¹⁰ (de Vries, 1900c, p. 845, 1950, p. 30)

Of the two antagonistic characters, Mendel calls the one visible in the hybrid the dominating, the latent one recessive. (de Vries, 1900a, p. 85, 1966, p. 111)

Corcos and Monaghan (1985) contend that de Vries, following Mendel's usage, attributed "dominant" (or "visible") and "recessive" (or "latent") to the morphological trait, while Bert Theunissen (1994) argues that de Vries replaced "active/latent" with Mendel's term "dominant/recessive" to designate the states of pagens. However, neither correctly reflects de Vries' subtle usage of "dominating/visible" and "recessive/latent" in 1900. As I have shown, Mendel mainly refers "dominant" and "recessive" to either the parental or hybrid trait with certain behaviour in the progeny. But for de Vries, the terms "dominant" and "recessive" are used to label two different pairs of things. On the one hand, de Vries refer these to the pair of morphological traits (*caractères*, *Merkmal*).

In the hybrid the simple differential character [*caractère*] from one of the parents is accordingly visible or dominant while the antagonistic character [*caractère*] is in the latent condition or recessive. (de Vries, 1900c, p. 845, 1950, p. 30)

The antagonistic characters [*caractères*] ordinarily remain combined during all of the vegetative life, one dominant, the other latent. (de Vries, 1900c, p. 845, 1950, p. 30)

The dominating and the recessive traits [*Merkmal*] are shown to be constant in the progeny, ... In this experiment they yielded an average of 77% with the dominating and 23% the recessive trait [*Merkmal*]. (de Vries, 1900a, p. 88, 1966, p. 114)

¹¹⁰ It is the paragraph in the paper that made Correns to realise that de Vries' already well knew Mendel's paper. In his paper (Correns, 1900, p. 159), Correns ironically indicates that de Vries used the same terms as Mendel in describing the paired traits was "a strange coincidence (*einen merkwürdigen Zufall*)."

On the other hand, de Vries refers those to the pair of hereditary characteristics (*Eigenschaften*), or qualities¹¹¹ (*qualités*).

One can unify the whole of those results by supposing that the two antagonistic qualities [*qualities*], dominant and recessive, are distributed [mutually exclusively] in equal parts to the pollen just as to the ovules. (de Vries, 1900c, p. 847, 1950, p. 32)

Of the two antagonistic [characteristics¹¹² (*Eigenschaften*)], Mendel calls the one visible in the hybrid the dominating, the latent one recessive. (de Vries, 1900a, p. 85, 1966, p. 111)

The individuals d and d² have only the dominating [characteristics (*Eigenschaft*)], those of r and r² constitution possess only the recessive [characteristics (*Eigenschaft*)], while the dr plants are obviously hybrid. (de Vries, 1900a, p. 86, 1966, p. 112)

Neither *Eigenschaften* (or *qualities*) nor *Merkmal* (or *caractères*) can be simply conflated. The word *Merkmal*, also used by Mendel, generally refers to what nowadays we call the morphological trait, while *Eigenschaften* was originally used by de Vries in his book *Intracellular Pangenesis* (1889) to denote the hereditary property, which can be passed onto the next generation. Therefore, de Vries' usage of "dominating/recessive" is genuinely different from Mendel's.

What is more, it is worth noting that de Vries' interchangeable usage of "dominant/recessive" with "visible (active)/latent" is not trivial. In *Intracellular Pangenesis* (1889), de Vries originally attributed the terms "active" and "latent" to two states of pangens. According to the theory of pangenesis, a pangen is the bearer of hereditary characteristics. Every hereditary characteristics, no matter in how many species it may be found, has its special kind of pangen. All living

¹¹¹ De Vries uses the word *Eigenschaften* in (1900a) and *qualités* in (1900d). It should be noted that in the book (1889), de Vries uses *Eigenschaften* to refer to hereditary characteristics or qualities.

¹¹² Evelyn Stern's translations of *Eigenschaften* (de Vries, 1966) are inconsistent. It is translated as characteristics in some places, while it is translated as characters in others (see Appendix 3). In order to distinguish *Eigenschaften* from *Merkmal* (and *Charakter*), I find that characteristics is a better translation, which is also consistent with de Vries' (1889) usage of *Eigenschaften* to denote the hereditary quality (Gager's translation (de Vries, 1910)).

protoplasm is built up of pangens. In the nucleus every kind of pangen of the given individual is represented; the remaining protoplasm in every cell contains chiefly only those that are to become active in it. With the exception of those kinds of pangens that become directly active in the nucleus, as for example those that dominate nuclear division, all the others have to leave the nucleus in order to become active. But most of the pangens of every sort remain latent in the nuclei, where they multiply, partly for the purpose of nuclear division, partly in order to pass on to the protoplasm. This delivery always involves only the kinds of pangens that have to begin to function. During this passage they can be transported by the currents of the protoplasm and carried into the various organs of the protoplasts. In short, a pangen has two states: active and latent. When it is in the active state, it moves from the nucleus to the cytoplasm to manifest its characteristics. When in the latent state, it remains in the nucleus with its characteristics “latent”. Therefore, de Vries’ usage of “dominating/recessive” (1900a, 1900c, 1900d) is also different from his original usage of “active/latent” (1889).

Table 10

Mendel’s and de Vries’ usages of “dominant” and “recessive”				
	Mendel (1865)		de Vries (1889)	de Vries (1900a, 1900c, 1900d)
Morphological traits with a certain behaviour	dominant /recessive (as a parental trait)	dominant /recessive (as a hybrid trait)		
Morphological traits	dominant/recessive (very occasionally)			dominant (visible)/recessive (latent)
Hereditary characteristics				dominant/recessive
Pangens (unit)			active/latent	

Given Mendel’s usage (1865) of “dominant/recessive” and de Vries’ usage (1889) of “active/latent” (see Table 9), de Vries’ interchangeable usage (1900a, 1900c, 1900d)

can be seen as an incomplete attempt of incorporating Mendel's terminology. Since de Vries' aim (1900a, 1900c) was to test the principle that the character of an organism is built up of distinct units, it is easily to infer from de Vries' book (1889) that units should be construed as pangens, though he does not enunciate this point in the 1900 papers. Thus, it can be expected that if de Vries introduces the conceptions of "dominant" and "recessive" to refer to the morphological traits, there are corresponding hereditary characteristics. This is exactly what de Vries did in the 1900 papers. But there was a difficulty for de Vries to explain the pattern of inheritance of dominant/recessive traits in terms of units or pangens. De Vries was hesitant to conflate "dominant/recessive" with "active/latent" to denote the state of a pangen. All that de Vries (1900a, 1900c, 1900d) conclusively showed is that the pollen grains and ovules having one characteristics in the formation behave in accord with the law of probability. This is why in the German paper de Vries is more modest¹¹³ in the conclusion by arguing that the law of segregation "has a basic significance for the study of the units which the species character is composed". (de Vries, 1966, p. 117) He well recognised that the principle that the specific characters of organisms are composed of units was yet well established by his hybridising experiments, though at that time he must have been optimistic on that the law of segregation and his Mendelian analysis of the hybridizing experiments would be very helpful to confirm the theory of pangenesis. Three years later, de Vries made a more comprehensive incorporation in the book (1903). Over one third of the book focuses on "the Mendelian laws of segregation."

Eventually, as Meijer indicates, "[de Vries] did not succeed in accommodating [Mendel's work] in to his already existing findings and views." (Meijer, 1985, p. 223) Shortly after de Vries abandoned his incorporating project by dismissing the significance of Mendel's work. As he wrote to Bateson on October 30th, 1901,

... [I]t becomes more and more clear to me that Mendelism [as the law of segregation] is an exception to the general rule of crossing. It is in no way

¹¹³ In the first French paper (1900c), de Vries boldly concludes that his hybridizing experiments "confirms that principles that I have expressed concerning the specific characters considered as being distinct units". (de Vries, 1950, p. 32)

the rule! It seems to hold only good in derivative cases, such as real variety-characters. (Provine, 1971, p. 68)

This letter well reflects a fact that, for de Vries, the significance of the law of segregation, if there is any, is its evidential support for his theory rather than being a rediscovery of an “old” law. Thus, his efforts are definitely better characterised as an incorporation than a rediscovery. Hence, it is hardly clear that de Vries’ 1900 papers are a rediscovery of Mendel’s laws, nor can they be characterised as a rediscovery.

Summary

None of de Vries’, Correns’ and Tschermak’s publication in 1900 can be simply characterised as a rediscovery of Mendel’s work. De Vries, Correns and Tschermak had different research problems from Mendel’s. Mendel’s work were not literally rediscovered or reintroduced, though de Vries, Correns, and Tschermak all learnt from Mendel’s work both conceptually and methodologically to solve their problems. In particular, I have shown that Mendel’s terminology, such as the concepts “dominant” and “recessive”, though adopted by de Vries, Correns, and Tschermak, was used in substantially different ways. In conclusion, I argue that all their practices should be better characterised as the attempts of incorporation of Mendel’s work with their own research project.

4.3 The Great Incorporation: When Mendel Met Heredity

Both de Vries and Tschermak recognised the significance of Mendel's work on *Pisum* in the study of heredity, but there was no phrase like "Mendel's theory of inheritance" in their publications or others in 1900. As shown in the section 4.2, de Vries (1900a, 1900c) was explicit on point that Mendel's work on *Pisum* is important for his theory of pangenesis, although he did not literally highlight the significance of Mendel's work to the study of heredity. Tschermak (1950, p. 44) also enunciated that "[Mendel's principle] proves to be of the highest significance for the study of inheritance," but he was implicit on in what sense Mendel's principle is important. The first explicit statement about the role of Mendel's work in the science of inheritance was made by Charles Davenport. In his paper "Mendel's Law of Dichotomy in Hybrids" (1901), based on Galton's three categories of inheritance¹¹⁴, Davenport is clear on the point that Mendel's law is a law of alternative inheritance.

[Mendel's] law of dichotomy in hybrids applies only to the second class, - alternative heritage, - although it has recently been brought forward by De Vries (1900) as the almost universal law of inheritance in hybrids... It has been rediscovered by De Vries and Correns, both of whom are able to add new evidence of its validity (for *alternative* heritage!). (Davenport, 1901, p. 307)

In addition, Davenport also reformulates the law of dichotomy in hybrids (i.e. de Vries' law of segregation) by adopting Galton's terminology.

1. Of the two antagonistic peculiarities the hybrid exhibits only one; and it exhibits it completely, so as not to be distinguishable in this regard from one of the parents. Intermediate conditions do not occur [in alternative heritage].
2. In the formation of the pollen and the egg cell the two antagonistic peculiarities are segregated; so that each ripe germ cell carries either one of these peculiarities. (Davenport, 1901, pp. 307–308)

¹¹⁴ Galton (1889, pp. 12–13) categorises the phenomena of inheritance into three classes: blending heritage, alternative heritage, and mixed heritage.

It is noticeable that Davenport's translation of *Eigenschaften* is slightly different from Stern's (de Vries, 1966). He uses the term "peculiarities", which was a term used by Galton (1889) to designate hereditary property¹¹⁵. It is clear that Davenport's formulation is an incorporation of de Vries' formulation of the law of segregation and Galton's general study of inheritance.

One year later W. F. R. Weldon made a similar incorporation by understanding Mendel's work as the laws of alternative inheritance.¹¹⁶ In his paper "Mendel's Law of Alternative Inheritance in Peas" (1902), Weldon identifies Mendel's laws with the law of dominance and of segregation. The law of dominance is formulated as follows.

If peas of two races be crossed, the hybrid offspring will exhibit only the dominant characters of the parents; and it will exhibit these without (or almost without) alteration, the recessive characters being altogether absent, or present in so slight a degree that they escape notice. (Weldon, 1902, p. 229)

The law of segregation is formulated as follows.

If the hybrids of the first generation, produced by crossing two races of peas which differ in certain characters, be allowed to fertilise themselves, all possible combinations of the ancestral race-characters will appear in the second generation with equal frequency, and these combinations will obey the Law of Dominance, so that characters intermediate between those of the ancestral races will not occur. (Weldon, 1902, p. 229)

In contrast to Davenport's paper, Weldon's paper primarily aims to criticise the universal validity of Mendel's laws to describe the phenomena of alternative inheritance.

In 1902, just a few months after Weldon's publication of his paper, William Bateson made a defence of the incorporation of Mendel's work with the study of heredity.

¹¹⁵ In his book (1889), Galton uses the term "peculiarity" to designate hereditary property rather than hereditary material. The statement that "[i]t may be that some natural peculiarity does not appear till late in life" (Galton, 1889, p. 5) is one good piece of evidence.

¹¹⁶ Davenport's paper (1901) was not cited in Weldon's paper (1902).

Compared with Davenport's and Weldon's articulation, Bateson's book *Mendel's Principles of Heredity: A Defence* was the first serious attempt in the history to introduce Mendel's study of *Pisum* to the study of heredity. By "serious" I mean that Bateson was very explicit on the point that Mendel's work on *Pisum*, especially the application of his principle, "may be extended from hybridisation to heredity in general". (Bateson, 1902, p. 35)

Bateson identifies that the aim of the study of heredity is to study both the "inward nature" and "outward" phenomena of heredity.

We want to know the whole truth of the matter; we want to know the physical basis, the inward and essential nature, "the causes", as they are sometimes called, of heredity; but we want also to know the laws which the outward and visible phenomena obey. (Bateson, 1902, pp. 2–3)

However, by the beginning of the 20th century though there were considerable observations and studies of the visible phenomena, few made noticeable contribution to understand the physical basis of heredity. The real problem seemed to Bateson was not only the ignorance of the essential nature of heredity, but also no one provided a reliable way of studying it. In his words, "no one has the remotest idea how to work on that part of the problem". (Bateson, 1902, p. 3) A breakthrough, recognised by Bateson, occurred with the publication of de Vries' papers (1900a, 1900c). More precisely speaking, Bateson would be rather happy to accept that "a marked step forward" was in fact made by Mendel. Bateson optimistically claimed that Mendel's work would "certainly play a conspicuous part in all future discussions of evolutionary problems", especially of the problems of heredity.

[T]here is no doubt we are beginning to get new lights of a most valuable kind on the nature of heredity and the laws which it obeys. (Bateson, 1902, p. 16)

But, Bateson did not simply apply Mendel's work to the problems of heredity. Rather he made a serious incorporation of Mendel's work with "modern knowledge", especially by formulating Mendelian conceptions and principles. What

is more, Bateson aims to defend these principles and their significance in the study of heredity against the objections from Weldon. The following quoted passage, I believe, well symbolises the beginning of a new science, genetics, or Mendelian genetics.

As regards the Mendelian principles, which it is the chief aim of this introduction to present clearly before the reader, a professed student of variation will easily be able to fill in the outline now indicated, and to illustrate the various conceptions from phenomena already familiar. To do this is beyond the scope of this short sketch. But enough perhaps has now been said to show that by the application of those principles we are enabled to reach and deal in a comprehensive manner with phenomena of a fundamental nature, lying at the very root of all conceptions not merely of the physiology of reproduction and heredity, but even of the essential nature of living organisms; and I think that I used no extravagant words when, in introducing Mendel's work to the notice of readers of the Royal Horticultural Society's Journal, I ventured to declare that his experiments are worthy to rank with those which laid the foundation of the Atomic laws of Chemistry. (Bateson, 1902, p. 35)

Summary

To sum up, the rediscovery story distorts the history of the origin of genetics from 1865 to 1902. Firstly, in contrast to what they maintained, I have argued that de Vries, Correns, and Tschermak in fact all read Mendel's paper before the completion of their research, and Mendel's paper influenced their "rediscovery" papers substantially. Secondly, by carefully analysing the "rediscovery" papers and their historical research context, I have shown that de Vries', Correns', and Tschermak's papers well reflect the attempts to incorporate Mendel's work with their researches both in the methodological and terminological senses rather than the rediscovery of (or reintroduction to) Mendel's work. The incorporation of Mendel's work with the study of heredity was further found in Davenport's, Weldon's, and especially Bateson's papers. Thus, I argue that the historical process of how Mendel's work was introduced to the science of

heredity should be characterised as an incorporation than as a rediscovery.

5

Exemplarising the Prelude of Genetics

In this chapter, I shall introduce an exemplar-based analysis of the origin of genetics. Firstly, on the basis of my historical interpretation, I shall highlight the inadequacies of the theory-driven analysis of the origin of genetics and of naïve Kunian characterisation. Secondly, I shall take the exemplar-based approach, introduced in the section 2.2, to analyse Mendel's work on *Pisum* (1865). Thirdly, I shall analyse de Vries' (1900a, 1900c, 1900d) and Correns' (1900) work in the same way. Fourthly, based on my analyses, I shall argue that the origin of genetics from Mendel to Bateson is best characterised as a chain of exemplary practices. Fifthly, I shall show that my exemplar-based analysis is also helpful to solve the problem of long neglect.

5.1 The Problems of the Theory-Driven Analysis of Mendel and the Rediscoverers

As I have mentioned in Chapter 1, philosophers used to pay insufficient attention to the origin of Mendelian genetics. What is Mendel's contribution to the origin of Mendelian genetics? What role does Mendel's work play in the "rediscovery" in 1900? What is the rediscoverers' contribution to the origin of Mendelian genetics? These questions were seldom articulated except in Ruse's brief summary of the origin of genetics.

Mendel's own work, as is well known, went practically unnoticed for thirty years. However, after its rediscovery at the beginning of [the 20th] century, a theory of heredity based on his ideas was developed in great depth and at a rapid speed. (Ruse, 1973, p. 12)

Ruse's statement is very succinct, but it is clearly rooted in a theory-driven understanding. The origin of genetics from Mendel to the rediscoverers, for many philosophers like Ruse (1973), is basically a process of the development of a theory. In order to make a fair assessment of the theory-driven account of the origin of genetics, I find it necessary to reconstruct it in detail based on my historical interpretation in the last two chapters. Remember the theory-driven "recipe" for analysing the history of science is like the following:

One should first analyse the history of a science by identifying a central explanatory theory. Then for that theory, one need to analyse its central concepts and principles (or laws) in different periods, details how they can be applied to explain the phenomena, reconstructs how they develop and are justified, and explores the strategies for theoretical changes.

So, if we follow the theory-driven approach, then the analysis of the origin of genetics should begin with identifying a theory of genetics. Thus, Mendel's, de Vries', Correns', and Bateson's work can be identified with the different versions of the theory of genetics. In order to understand the origin of the theory of genetics, we have to detail the theoretical variations of these different versions of the theory. Given that Mendel's work is about development of hybrids in their progeny, it is natural to argue that Mendel's major contribution is to propose a theory of hybrid development. In 1900 de Vries developed Mendel's theory by extending its applicability and refining the law. In the same year, Correns also reformulated Mendel's theory by merging Mendel's laws in terms of anlagen.

The Main Theoretical Changes from Mendel to Bateson			
The Version of the theory of Genetics	The Cellular Factor relating to Trait	Relation of Cellular Correspondent-Trait	Applicability of Mendel's Law
Mendel's Version	Kinds of cell	Correspondence	Pisum, Phaseolus, etc

De Vries' Version	Characteristics	Determination	All true hybrids
Correns' Version	Anlagen	Determination	Some hybrids
Bateson's Version	Allelomorphs	Determination	Certain phenomena of alternative inheritance

It can be argued that there are two significant modifications to Mendel's theory made by de Vries and Correns. One is that the correspondence between kinds of cell and morphological traits in Mendel's work was replaced with a kind of determination in de Vries' and Correns' work. The other is that the interfiled connection of the theory is advanced. Mendel's "kinds of cell" in fertilisation was reconceptualised as "characteristics" in the formation of pollen and ovules (de Vries, 1900a, 1900c, 1900d) or "anlagen" in the process of the fusion of the reproductive nuclei (Correns, 1900). Three years later, inspired by de Vries' and Correns' work, Bateson further developed the theory by refining the applicability and key concepts. Thus, the "essence" of the origin of genetics from Mendel to Bateson is characterised as a process of the development of a theory.



However, this characterisation is highly problematic. Firstly, if the "essence" of the origin of genetics is depicted as the development of a theory, it is extremely difficult to identify such a theory. As I have emphasised repeatedly, Mendel's work is not about heredity, while de Vries' and Correns' concern were not about development of hybrids in their progeny. As shown in Chapter 3, de Vries, Correns, and Tschermak in their 1900 papers had all different concerns. In particular, it is difficult to maintain if they proposed their theories explicitly, especially in Tschermak's case. Tschermak attempted to incorporate Mendel's analysis of the progeny of hybrids with his theory of regular differential valency of traits, though he did not have any sophisticated formulation in 1900. Thus, it is not obvious that there is a linear development of a theory from Mendel (1865) to Tschermak (1900a, 1900b). Correns aimed to test Mendel's work on *Pisum* experimentally, and ended up by proposing a Mendelian Rule. De Vries proposed the law of segregation and

intended to use it to support his theory of pangenesis. So, it is not historically accurate to summarise de Vries' and Correns' work as the development or revision of Mendel's theory of hybrid development, given that their concerns are not the development of hybrids in their progeny.

Secondly, even if Correns' Mendelian Rule and de Vries' law of segregation can be construed as revised versions of Mendel's theory, such a theory-driven analysis of the origin of genetics fails to reflect the radical change of the subject of the theories. Accordingly, some more complicated problems occur: What makes Mendel's theory of hybrid development and de Vries' theory different versions of a theory? What is the connection between Mendel's and de Vries' theories? An adequate analysis of the origin of genetics has to articulate the change from the theory of hybrid development to of heredity. There is much more to be done if one tries to defend the view that there was a development of the theory of Mendelian genetics from Mendel to Bateson.

Thirdly, the theory-driven analysis of the origin of genetics from Mendel to the rediscoverers faces the problem of practice¹¹⁷. As I shall discuss in detail in the section 5.3, Mendel's work is much more than a theoretical construction, so are the rediscoverers'. The rediscoverers' work is heavily influenced by the non-theoretical aspect of Mendel's. The non-theoretical aspect of the origin of genetics is missing and largely neglected from the theory-driven analysis.

In short, it can be concluded that the theory-driven approach to analysing the origin of genetics is inadequate. In the next two sections, I shall introduce an alternative way to analysis the origin of genetics from Mendel to Bateson by taking the exemplar-based approach.

¹¹⁷ For the explication of the problem of practice, see the section 1.2.

5.2 Mendel's Exemplary Practice on *Pisum*

As I have outlined in the section 2.3, the first step to analyse the practice of a scientist (or a community of scientists) in the history is to identify his initial research problem and the research context. In Chapter 3, I have shown that Mendel is very explicit on his purpose of the study of *Pisum*: To study the development of hybrids in their progeny. (Mendel, 1865, p. 3) More specifically, the initial research problem for Mendel is:

MP1¹¹⁸. How could one “determine the number of different forms in which hybrid progeny appear, permit classification of these forms in each generation with certainty, and ascertain their numerical interrelationship”? (Mendel, 1865, p. 4)

Pre-Experiment Practice

In order to solve MP1, the first task for Mendel is to select the right experimental plant. (MG1) Thus, he sets three criteria for the ideal experimental plants.

MC1. The experimental plants must necessarily possess constant differing traits.

MC2. Their hybrids must be protected from the influence of all foreign pollen during the flowering period or easily lend themselves to such protection.

MC3. There should be no marked disturbances in the fertility of the hybrids and their offspring in successive generations. (Mendel, 1865, p. 5)

After carefully undertaking two-year experiments, Mendel decided to select *Pisum* as the experimental plants because all the three criteria are fulfilled:

1'. Some distinct forms of *Pisum* possess easily and reliably recognisable constant traits.

¹¹⁸ In this chapter, I shall use MPx to denote problem x, (for example, P1 for the problem 1), and MEx to experiment x, MHx to hypothesis x, MCx to concept x, MGx to practical guide x. (Note x represents number, and M represents Mendel's)

2'. The fertilising organs of *Pisum* are closely surrounded by the keel, and the anthers burst within the bud, so the stigma is covered with pollen even before the flower opens. The influence of foreign pollens is negotiable. (Only a very few among 10,000 in garden beds, while none found in the green house.)

3'. The offspring of hybrids are fertile.

The next task for Mendel is to select several pairs of differing traits. (MG2) For Mendel, any pair of differing traits to be experimented should be a sharp and definite contrast. (MC4) According to this criteria, seven pairs are chosen: the shape of the seed, the colour of the seed, the colour of the coat around the seed, the shape of the ripe pod, the colour of the unripe pod, the location of the flower, and the length of the stem. In addition, in order to prevent and observe the contamination with foreign pollen, Mendel plants most of peas in garden beds, while places a number of potted plants in a greenhouse during the flowering period in order to serve as controls for the main experiment in the garden against possible disturbance by insects (especially the beetle *Bruchus pisi*). (MG3)¹¹⁹

The Problem-Specification (MP1→MP2)

After the identification of the experimental plant and the pairs of differing traits, Mendel narrows down MP1 to a more specific sub-problem:

MP2. What are the changes for each pair of differing traits, selected in the pre-experiment practice, in the offspring of *Pisum*? Or, what is the law deducible from the changes for each pair of differing traits selected in the successive generations? (Mendel, 1865, p. 7)

This problem-specification is one important activity in problem-defining. It often reformulates a problem (or a part of a problem) into experimentally testable or/and conceptually more specific problems for the further investigation. Mendel's problem specification MP1 to MP2 is based on his pre-experiment practice, especially the identification of the experimental plant and the pairs of differing

¹¹⁹ As I shall discuss in the section 5.4, Tschermak also followed this practical guide in his crossing experiments.

traits.

Experiments 1, Conceptualisation, and Confirmation

In order to solve MP2, Mendel finds it necessary to break up the study into many separate experiments, as there are constantly differing traits in *Pisum*. The first series of experiments (ME1) are to cross the selected peas differing in one morphological trait (e.g. the colour of the seed). The results were amazing. Each of the seven morphological traits either resembles one of the two parental traits. For example, when the yellow and green peas are crossed, all the hybrids are yellow. No intermediate form is found. This result leads Mendel to define two key concepts “dominating traits” and “recessive traits” to describe the phenomena. The concept “dominating” designates the parental trait, which passes into hybrids entirely or almost entirely unchanged, while “recessive” designates the trait which becomes latent in hybrids. This conceptualisation is very important for Mendel because this pair of concepts is helpful to analyse the change of a pair of differing traits in the successive generations. In addition, the results of ME1 also make Mendel to confirm that confirm a rule (*Regel*) that hybrids do not represent the intermediate form between the parental traits, whether the dominating trait belongs to the seed or pollen plant.

Experiments 2 and the Redefinition of Dominating

The second series of experiments (ME2) are to cross the hybrids obtained from E1. In the first generation of the hybrids, the recessive traits reappear. By idealising the raw data, Mendel recognises that the ratio of the dominating trait to the recessive one is close to 3 : 1, as shown in Table 1. For example, when the yellow hybrids are crossed, three-fourths of the peas in the next generation are yellow, while the rest are green. This recognition well shows that Mendel, on the basis of the results of E2, modifies the concept “dominating”, which refers not only to a parental trait that would pass unchanged to all the offspring when self-fertilised, but also to a hybrid trait that would exhibit the same behaviour as it did in the first generation.

Experiments 3, Reconceptualising the 3 : 1 Ratio, and the Proposal of Hypothesis 1

The third series of experiments (ME3) are to cross the hybrids with the recessive traits obtained and the hybrids with the dominating traits obtained in ME2

respectively. The results are, that the offspring from those with the recessive traits are still with the recessive traits, whereas only one-third of the hybrids with the dominating traits have the offspring with dominating trait, and the rest have a mixture of the offspring with both dominating and recessive traits. For example, among 519 plants raised from the yellow peas in the first generation, 166 yielded yellow while 353 yielded yellow and green in the proportion 3 : 1. Based on these results, Mendel insightfully distinguishes two forms of those seemingly dominating traits in the F₂ generation: the dominating constant form and the dominating hybrid form. The dominating constant form is implicitly defined by Mendel as the trait, which would pass onto the progeny without any change. For example, all the offspring of yellow (as a dominating constant form) seeds must be yellow. On the other hand, the dominating hybrid form is implicitly defined as trait, whose progeny include both the seemingly dominating trait and the recessive trait. For example, some of the offspring of yellow (as a dominating hybrid trait) seeds are yellow, while others are green. Thus, Mendel categorises the morphological traits of *Pisum* into three classes: the dominating trait, the (dominating) hybrid trait, and the recessive trait. On the basis of the results in the F₁ and F₂ generations and newly refined concepts, Mendel proposes a hypothesis:

MH1. “of the seeds formed by the hybrids with one pair of differing traits, one half again develop the hybrid form while the other half yield plants that remain constant and receive the dominating and the recessive character in equal shares.” (Mendel, 1865, p. 17) (The law of development concerning a pair of differing traits)

In other words, the 3 : 1 ratio (of the dominating and recessive traits) in the F₁ generation is reconceptualised as the 1 : 2 : 1 ratio (of constant dominating, hybrid, and recessive traits).

Experiments n, Confirmation of MH1 and its Corollary

MH1 is confirmed by Mendel’s experiments on the subsequent generations from hybrids. In each generation the offspring of those with the hybrid trait split up into the dominant constant, hybrid, and recessive constant traits according to the ratios 1 : 2 : 1. Moreover, Mendel deduces a corollary from MH1:

MH1’. In the nth generation the distribution of the dominant constant, hybrid, and

recessive constant traits is the $2^{n-1} : 2 : 2^{n-1}$ ratio if “on the average, equal fertility for all plants in all generations, and if one considers, furthermore, that half of the seeds that each hybrid produces yield hybrids again while in the other half the two traits become constant in equal proportions.” (Mendel, 1865, p. 18)

Thus, according to MH', for each pair of differing traits, the traits in each generation is quantitatively classified with certainty and their numerical interrelationship is also determined. Therefore, MP2 is solved by an intertwined practice of ME1, ME2, ME3, MH1, MH1', and the conceptualization of “dominating constant trait”, “hybrid trait”, and “recessive constant trait.”

Generation	Dominating Constant	Hybrid	Recessive Constant
1	1	2	1
2	3	2	3
3	7	2	7
4	15	2	15
5	31	2	31
n	$2^n - 1$	2	$2^n - 1$

Problem Specification (MP1, MP2 \Rightarrow MP3) and Symbolic Denotation

After the resolution to MP2, Mendel makes another problem specification by shifting his focus to the behaviour of the multiple pairs of differing traits in the progeny of *Pisum*:

MP3. Is the law of development concerning a pair of traits (i.e. H1) still applicable when several traits are united in the hybrid of *Pisum* through fertilisation? (Mendel, 1865, p. 18)

As we can see, MP3 is formulated with the help of MP1, MP2, and MH1. In order to solve MP3, especially to make the analyse of the data simpler, Mendel denotes the traits symbolically by using a capital letter to denote a dominating constant trait, a lowercase letter to denote a recessive one, and a combination of a capital and

lowercase letters to a hybrid one. For example, suppose A denotes round shape, a wrinkled shape, B yellow albumen, b green albumen. Then a round yellow plant is denoted as AB, a wrinkled green one ab, and so on.

Experiments 1' and the Proposal of Hypothesis 2

Mendel designs two series of experiments to investigate MP3. The first series (ME1') is to cross the parental plants differed in seed shape and albumen colour. After fertilising the seeds from round yellow (AB) plants with the pollens from wrinkled green (ab) plants, Mendel obtains 315 round and yellow (AB) seeds, 101 wrinkled and yellow (aB) seeds, 108 round and green (Ab) seeds, and 32 wrinkled and green (ab) seeds. By planting these seeds, Mendel obtains nine different traits among the offspring of hybrids.

The Amount of Plants	The Traits	The Denotation of Traits
38	round and yellow	AB
35	round and green	Ab
28	Wrinkled and yellow	aB
30	Wrinkled and green	ab
65	Round yellow and green	ABb
68	Wrinkled yellow and green	aBb
60	Round yellow and wrinkled yellow	AaB
67	Round green and wrinkled green	Aab
138	Round yellow and green, and wrinkled yellow and green	AaBb

These seeds are classified by Mendel into three groups: The first group consists of the only constant traits (i.e. AB, Ab, aB, ab); the second group consists of the traits in the form of ABb, aBb, AaB, Aab, which are constant for one trait and hybrid for the other; the third group consists of the hybrid traits (i.e. AaBb). The ratio of the traits AB, Ab, aB, ab, ABb, aBb, AaB, Aab, and AaBb is idealised by Mendel as 1 : 1 : 1 : 1 : 2 : 2 : 2 : 2 : 4. Furthermore, Mendel insightfully recognises that the

combination of two kinds of differing traits in a series expression ($AB + Ab + aB + ab + 2ABb + 2aBb + 2AaB + 2Aab + 4AaBb$) can be obtained through a combination of the expressions ($A + 2Aa + a$) and ($B + 2Bb + b$). This makes Mendel to propose another hypothesis.

MH2. "The progeny of hybrids in which several essentially different traits are united represent the terms of a combination series in which the series for each pair of differing traits are combined... [T]he behaviour of each pair of differing traits in a hybrid association is independent of all other differences in the two parental plants." (Mendel, 1865, p. 22) (The law of combination of differing traits)

Experiments 2' and the Confirmation of MH2

MH2 is also confirmed by Mendel's a further series of experiments (ME2') on three pairs of differing traits. By crossing the parental plants differing in the seed shape, albumen colour, and colour of seed coat, Mendel obtains the following results.

3 Constant Traits		2 Constant and 1 Hybrid Traits		2 Hybrid and 1 Constant Traits		3 Hybrid Traits	
8	ABC	22	ABCc	45	ABbCc	78	AaBbCc
14	ABc	17	AbCc	36	aBbCc		
9	AbC	25	aBCc	38	AaBCc		
11	Abc	20	abCc	40	AabCc		
8	aBC	15	ABbC	49	AaBbC		
10	aBc	18	ABbc	48	AaBbc		
10	abC	19	aBbC				
7	abc	24	Aabc				
		14	AaBc				
		18	AaBc				
		20	AabC				
		16	Aabc				

Again, Mendel indicates that the expression $(ABC + ABc + AbC + Abc + aBC + aBc + abC + abc + 2ABCc + 2AbCc + 2aBCc + 2abCc + 2ABbC + 2ABbc + 2aBbC + 2aBbc + 2AaBC + 2AaBc + 2AabC + 2Aabc + 4ABbCc + 4aBbCc + 4AaBCc + 4AabCc + 4AaBbC + 4AaBbc + 8AaBbCc)$ is a combination series of the expressions $(A + 2Aa + a)$, $(B + 2Bb + b)$, and $(C + 2Cc + c)$.

Moreover, Mendel deduces a corollary from MH2 to predict the number of different trait combination, of all the possible combinations, and of combinations that remain constant.

MH2'. If n designates the number of pairs of differing traits in the parental plants, then 3^n is the number of different trait combination, 4^n is the number of , 2^n is the number of combinations that remain constant. (Mendel, 1865, pp. 22–23)

As seen from Mendel's experiments, MH2' is well confirmed. For the parental plants differing one pair of differing traits, there are 3 ($=3^1$) different traits among the hybrids: the dominating constant, hybrid, and recessive constant traits; and 2 ($=2^1$) of them are constant traits. For the parental plants differing two pair of differing traits, there are 9 ($=3^2$) different trait combinations, and 4 ($=2^2$) of them include only constant traits. Furthermore, with the confirmation of MH2', MP3 is solved.

Problem Specification (MP1, MP2, MP3 \Rightarrow MP4)

Although with MH1, MH1', MH2, and MH2' Mendel could well determine "the number of different forms of the hybrid progeny, permit classification of these forms in each generation with certainty, and ascertain their numerical interrelationship", he still attempts to find a reductive explanation of these hypotheses.

MP4. How can MH1 and MH2 be explained in terms of seed and pollen cells?

A hypothesis is proposed by Mendel:

MH3. Pea hybrids form germinal and pollen cells that in their composition correspond in equal numbers to all the constant forms resulting from the combination of traits united through fertilisation. (Mendel, 1865, p. 29)

Experiments 1'', 2'', and the Hypothetico-Deductive Reasoning

In order to test H3 experimentally, Mendel makes some testable predictions by deducing from the following assumptions,

Premise 1. There are many kinds of germinal cells in the ovaries of hybrids; while there are many kinds of pollen cells in the anthers of hybrids. (Mendel, 1865, p. 24)

Premise 2. The germinal and pollen cells correspond in their internal make-ups to the individual forms. (Mendel, 1865, p. 24)

Premise 3. The constant traits can be produced when germinal and pollen cells are alike.

Premise 4. The seed plants for the experiments all have round shape (denoted as A) and yellow albumen (B), while the pollen plants all have wrinkled shape (a) and green albumen (b).

Premise 5. Four experiments are designed:

- (1) The hybrid seeds (i.e. with AB, Ab, aB, ab traits) are fertilised with the pollen from the plants with AB traits.
- (2) The hybrid seeds (i.e. with AB, Ab, aB, ab traits) are fertilised with the pollen from the plants with ab traits.
- (3) The seeds from the plants with AB traits are fertilised with the hybrid pollen (i.e. with AB, Ab, aB, ab traits).
- (4) The seeds from the plants with AB traits are fertilised with the hybrid pollen (i.e. with AB, Ab, aB, ab traits).

With premises 1, 4, and 5, it is inferable that during the fertilisation, there are corresponding kinds of germinal and pollen cells that develop and combine.

- (1) Germinal cells A'B', A'b', a'B', a'b' with pollen cells A'B'
- (2) Germinal cells A'B', A'b', a'B', a'b' with pollen cells a'b'

(3) Germinal cells A'B' with pollen cells A'B', A'b', a'B', a'b'

(4) Germinal cells a'b' with pollen cells A'B', A'b', a'B', a'b'

Mendel deductively infers that in the each of the four experiments, the following combinations of the cell-types will be expected and they are in equal ratio to each other.

$$(1) \frac{A'B'}{A'B'} : \frac{A'B'}{a'b'} : \frac{A'B'}{A'b'} : \frac{A'B'}{a'B'} = 1 : 1 : 1 : 1$$

$$(2) \frac{A'B'}{a'b'} : \frac{a'b'}{a'b'} : \frac{A'b'}{a'b'} : \frac{a'B'}{a'b'} = 1 : 1 : 1 : 1$$

$$(3) \frac{A'B'}{A'B'} : \frac{A'B'}{a'b'} : \frac{A'b'}{A'b'} : \frac{A'B'}{a'B'} = 1 : 1 : 1 : 1$$

$$(4) \frac{A'b'}{a'b'} : \frac{a'b'}{a'b'} : \frac{A'b'}{a'b'} : \frac{a'B'}{a'b'} = 1 : 1 : 1 : 1$$

Correspondingly, given the premises 2 and 3, the following traits are expected to stand in equal ratio to each other in each experiment.

$$(1) AB : AabB : ABb : aAB = 1 : 1 : 1 : 1$$

$$(2) AaBb : ab : Aab : aBb = 1 : 1 : 1 : 1$$

$$(3) AB : AaBb : ABb : AaB = 1 : 1 : 1 : 1$$

$$(4) AaBb : ab : Aab : aBb = 1 : 1 : 1 : 1$$

Moreover, in the experiments (1) and (3), since the dominating traits A and B appear in every combination, all seeds should be imprinted their characteristics. In other words, it is expected that all seeds obtained from experiments (1) and (3) are round and yellow. On the other hand, in the experiments (2) and (4), it is expected that there are four kinds of seeds obtained: round yellow, round green, wrinkled yellow, and wrinkled green.

By undertaking these four experiments, Mendel obtains the favourable results (see Table 11). All seeds obtained in the experiments (1) and (3) are exclusively round and yellow. On the other hand, the amount of the round yellow, round green, wrinkled yellow, and wrinkled green seeds are observed approximately in equal

number from the experiments (2) and (4).

Table 11

Experiment (1)	Experiment (2)	Experiment (3)	Experiment (4)	Morphological Traits
98	31	94	24	round yellow seeds
0	26	0	25	round green seeds
0	27	0	22	wrinkled yellow seeds
0	26	0	27	wrinkled green seeds

Therefore, Mendel confirms MH3. From a philosopher's point of view, this is a perfect case of the hypothetico-deductive reasoning, which is normally in the form that e HD-confirms h relative to k if and only if $h \wedge k \models e$ and $k \not\models e$. In Mendel's case, we have seen that the results of ME 1'' HD-confirms MH3 relative to Premise 1, 2, 4, as $MH3 \wedge \text{Premise 1} \wedge \text{Premise 2} \wedge \text{Premise 4} \models \text{the results of ME1''}$ and $\text{Premise 1} \wedge \text{Premise 2} \wedge \text{Premise 4} \not\models \text{the results of ME1''}$.

Furthermore, when the seeds (with the cell-types $\frac{A'B'}{A'B'}, \frac{A'B'}{A'b'}, \frac{A'b'}{a'B'}, \frac{A'b'}{a'b'}$) obtained from experiments (1) and (3) are sown, it can be predicted that the cell-types of the seeds harvested in the following year are:

$$\frac{A'B'}{A'B'}, \frac{A'B'}{A'b'}, \frac{A'b'}{A'B'}, \frac{A'b'}{A'b'}, \frac{A'B'}{A'b'}, \frac{A'b'}{A'B'}, \frac{A'B'}{a'B'}, \frac{A'b'}{a'B'}, \frac{A'B'}{a'b'}, \frac{A'b'}{a'b'}, \frac{A'b'}{A'b'}, \frac{A'b'}{a'B'}, \frac{A'b'}{a'b'}, \frac{A'b'}{A'b'}, \frac{A'b'}{a'B'}, \frac{A'b'}{a'b'}$$

Thus, the traits of the seeds in each group are expected to be round and yellow (AB); round yellow and green seeds (ABb); round and wrinkle yellow seeds (AaB); and round and wrinkle, yellow and green seeds (AaBb). And the amount of the seeds in each group is approximately equal. Again, this prediction is confirmed (see Table 12).

Table 12

Experiment 1	Experiment 3	Morphological Traits
20	25	Round yellow seeds (AB)
23	19	Round yellow and green seeds (ABb)
25	22	Round and wrinkled yellow seeds (AaB)
22	21	Round and wrinkled, yellow and green seeds (AaBb)

Furthermore, MH3 is also hypothetico-deductively confirmed by the experiments 2'', in which Mendel tests the traits of flower colour and stem length. Therefore, MP4 is solved.

Symbolic Reconceptualisation of MH1, MH2, and MH3

With the help of symbolic denotation, MH1 can be easily reformulated in the expression that

$$A + 2Aa + a$$

where A denotes the dominating constant trait, Aa the hybrid trait, and a the recessive constant trait.

Similarly, an application of MH2 to the case of two pairs of differing traits can be expressed in the way that

$$(A + 2Aa + a)(B + 2Bb + b) = AB + Ab + aB + ab + 2aBb + 2AaB + 2Aab + 4AaBb$$

where B denotes a different dominating trait, Bb a hybrid trait, and b a corresponding recessive constant trait.

Moreover, the explanation of H1 in terms of H3 can be expressed as

$$\frac{A'}{A'} + \frac{A'}{a'} + \frac{A'}{a'} + \frac{a'}{a'} = A + 2Aa + a$$

The explanation of MH2 in terms of MH3 in the case of two pairs of differing traits is reformulated as

$$\begin{aligned}
& \frac{A'B'}{A'B'} + \frac{A'B'}{a'b'} + \frac{A'B'}{a'B'} + \frac{A'B'}{a'b'} + \frac{A'b'}{A'B'} + \frac{A'b'}{A'b'} + \frac{A'b'}{a'B'} + \frac{A'b'}{a'b'} + \frac{a'B'}{A'B'} + \frac{a'B'}{A'b'} + \frac{a'B'}{a'B'} \\
& + \frac{a'B'}{a'b'} + \frac{a'b'}{A'B'} + \frac{a'b'}{a'B'} + \frac{a'b'}{a'B'} + \frac{a'b'}{a'b'} \\
& = AB + ABb + AaB + AaBb + ABb + Ab + AaBb + Aab + AaB \\
& + AaBb + aB + aBb + AaBb + Aab + aBb + ab \\
& = AB + Ab + aB + ab + 2ABb + 2aBb + 2Aab + 2AaB + 4AaBb
\end{aligned}$$

Summary and Remarks

I have shown that Mendel's work on *Pisum* can be well characterised as an exemplary practice in the study of the development of *Pisum* by contextually problem-defining, conceptualisation, experimentation, hypothesisation, and reasoning, as summarised in Table 13.

Table 13

Mendel's Exemplary Practice on <i>Pisum</i>					
Research Problems	Vocabulary	Practical Guides	Hypothesi sation	Experim ents	Patterns of Reasoning
MP1 MP2 MP3 MP4	Dominating constant trait (A) Recessive constant trait (a) Hybrid trait (Aa) Kinds of germinal Cell (e.g. A') Kinds of pollen Cell (e.g. a')	MG1. The selection of experimental plants (MC1, MC2, MC3) MG2. The selection of morphological traits of peas (C4) MG3. Other pre-Experimental procedures (e.g. places of growing) Experimental Procedures for Various Experiments	MH 1 MH 1' MH2 MH2' MH3	ME1 ME2 ME3 ME _n ME1' ME2' ME1'' ME2''	H-D confirmation

5.3 The Rediscoverers' Exemplary Practices

de Vries' Exemplary Practice

As I have discussed, de Vries' papers (1900a, 1900c, 1900d) are part of his project of testing his theory of pangenesis. The initial problem (DP1) for de Vries is to experimentally test the principle (DH1) that the specific characters of organisms are composed of distinct units. (de Vries, 1900a, pp. 83–84, 1900c, p. 845) It should be noted that DH1 is a reformulated version of the hypothesis (DH1') in the theory of pangenesis (de Vries, 1889) that every hereditary characteristic has its special kind of pangen.

The Problem-Specification (DP1 → DP2) and the Conceptualisation of Traits

In order to investigate DP1, de Vries begins with the simplest case by examining the hybrid plants differing in a pair of antagonistic traits. (DG1) This is a Mendel's legacy for de Vries' research.

DP2. What is the change of a pair of antagonistic traits of hybrid?

Moreover, de Vries adopts Mendel's terminology to classify antagonistic traits, though in a different way¹²⁰. One of the two antagonistic characteristics is called the dominating characteristic, while the other the recessive.

Hypothesisation

In order to deduce testable hypotheses, de Vries makes the following assumptions.

DH2. In the hybrids two antagonistic characteristics lie next to each other.

DH3. In vegetative life only the dominating characteristics is visible.

DH4. In the formation of pollen grains and ovules these characteristics separate and behave independently.

DH5. The pollen grains and ovules of monohybrid have the pure characteristic one of the parents.

¹²⁰ See my in-depth discussion on this distinction in section 4.2.

At first glance, these hypotheses are confusing. In the paper, de Vries makes some seemingly inconsistent statements. For example, one of the two conclusions drawn from the experiments by de Vries is that “[o]f the two antagonistic characteristics, the hybrid carries only one” (de Vries, 1900a, p. 84, 1966, p. 110), while it is also assumed that “[i]n the hybrid the two antagonistic [characteristics] lie next to each other” (de Vries, 1900a, p. 85, 1966, p. 111). Does the hybrid carry one characteristic or two at all? In addition, some statements are a bit confusing. For example, DH2 states that in the hybrids two antagonistic characteristics lie next to each other. How can the hereditary characteristics “lie next to each other” in the cell? In order to fully understand and clarify de Vries’ reasoning, I find it necessary to reformulate the argument by relating the 1900 papers with the book.

As I have introduced, pangens, the independent hereditary units, are the carriers of hereditary characteristics. Since de Vries never mentioned the term “pangen” in the 1900 papers, this well reflects his caution¹²¹. DH2 can be reformulated as the hypothesis that

DH2’. In the hybrids the pangens carrying two antagonistic characteristics lie next to each.

Correspondingly, DH3 can be reformulated in the way that

DH3’. In vegetative life, only the pangen carrying the dominating characteristic is active.

DH4 can be reformulated in the way that

DH4’. In the formation of pollen grains and ovules these pangens separate.

On the basis of DH1’, DH2’, DH3’, DH4’, de Vries uses a mathematical model (“law of probability” in his words) to explicate the formation of pollen grains and ovules as follows.

$$\text{DH6. } (d + r)(d + r) = d^2 + 2dr + r^2$$

¹²¹ It has already been recognized by Meijer “From 1889 onwards [de Vries] published a large number of papers related to pangenesis, but he hardly ever mentioned pangenesis explicitly unless he was confident of having found conclusive evidence for one of its premises.” (Meijer, 1985, p. 203)

where d represents the pangen carrying the dominating characteristic, while r the recessive one. This mathematical model is an indispensable hypothesis in de Vries' papers, since it implicitly suggests that in the offspring of the hybrids, two pangens still next to each other. The seeds with two pangens both carrying the dominating characteristics have the dominating trait, those with two pangens both carrying the recessive ones have the recessive trait, while the seeds with two pangens carrying two antagonistic characteristics have the dominating trait. Moreover, (DH6') the ratio of these combinations of pangens is 1 : 2 : 1. Correspondingly, (DH6'') the ratio of the dominating trait to the recessive one is 3 : 1.

The Confirmation of DH6''

This testable hypothesis (DH6'') is widely (hypothetico-deductively) confirmed by the results of de Vries' crossing experiments. (See Table 14)

Table 14

DE1. De Vries' Data on the Crossing Experiments (1900a, 1900c)			
Parent with dominant character	Parental with the recessive character	Proportion of hybrids with the recessive character	Year of Crossing
<i>Agrostermma Githgao</i>	<i>Agrostermma nicaeensis</i>	24%	1898
<i>Chelidonium majus</i>	<i>Chelidonium laciniatum</i>	26%	1898
<i>Coreopsis tinctoria</i>	<i>Coreopsis brunea</i>	25%	1896
<i>Datura Tabula</i>	<i>Datura Stramonium</i>	28%	
<i>Hyoscyamus niger</i>	<i>Hyoscyamus pallidus</i>	26%	1898
<i>Lynchnis diurna</i>	<i>Lynchnis vespertina</i>	27%	1892
<i>Lynchnis vespertina</i>	<i>Lynchnis glabra</i>	28%	1892

<i>Oenothera Lamarckiana</i>	<i>Oenothera Brevistylis</i>	22%	1898
<i>Solanum nigrum</i>	<i>Solanum chlorocarpum</i>	24%	1894
<i>Trifolium pratense</i>	<i>Trifolium album</i>	25%	
<i>Veronica longifolia</i>	<i>Veronica alba</i>	22%	1899

Another testable hypothesis proposed by de Vries' is that when crossing a hybrid with the pollen of one of the two parents (or in reverse), one would obtain the offspring with the combination of pangens expressed mathematically as follows.

$$\text{DH7. } (d + r)d = d^2 + dr$$

or

$$(d + r)r = dr + r^2$$

The empirical interpretation of DH7 is that:

DH7'. The offspring of the hybrid seeds with the pollens of one of the two parents have two combinations of pangens: One is with two pangens both carrying the same one parental characteristic, while the other is with two pangens carrying two parental characteristics each.

A testable interpretation is:

DH7''. Half of the offspring of the hybrid seeds with the pollens of one of the two parents have one of the two parental traits, while the other half have the hybrid trait (i.e. the dominating trait). In other words, the ratio of the dominating trait to the recessive one is 1 : 1 in the case of $(d + r)r = dr + r^2$, while in the case of $(d + r)d = d^2 + dr$, all the offspring exhibit the dominating trait.

The Confirmation of DH7''

DH7'' is (hypothetico-deductively) confirmed by several crossing experiments. (See Table 15)

Table 15

DE2. De Vries' Data on the Back-Crossing Experiments (1900a, 1900c)			
Parent with dominant character	Parental with the recessive character	Proportion of hybrids with the recessive character	Year of Crossing
<i>Clarikia pulchruella</i>	<i>Clarikia white</i>	50%	1896
<i>Oenothera Lamarckiana</i>	<i>Oenothera brevistylis</i>	25%	1895
<i>Silene Armeria</i>	<i>Silene white</i>	22%	1895

On the basis of his hypotheses (DH2, DH3, DH4, and DH5) and experimentally confirmed hypotheses (DH6'' and DH7''), de Vries concludes that DH1 is well confirmed.

Therefore, de Vries' exemplary practice can be summarised as:

Table 16

De Vries' Exemplary Practice on <i>Character-Unit</i>					
Research Problems	Vocabulary	Practical Guides	Hypotheses	Experiments	Patterns of Reasoning
DP1 DP2	Dominating trait (A) Recessive trait (a) Dominating characteristic Recessive characteristic Units	DG1	DH1 DH1' DH2 DH2' DH3 DH3' DH4' DH5 DH6 DH6' DH6'' DH7 DH7' DH7''	DE1 DE2	H-D confirmation

Correns' Exemplary Practice

As I have argued in the section 4.1, Correns' initial concern is the xenia question.

CP1. Does foreign pollen have a direct influence on the characteristics of the fruit and seed?

In 1896 Correns began studying this problem in the case of *Pisum*. The purpose of the paper, as I have argued, is to test Mendel's work on *Pisum*. Thus, CP1 is specialised into another problem.

CP2. Is Mendel's observation and the law on *Pisum* verifiable?

In order to test Mendel's observation and analysis, Correns follows Mendel to focus on a pair of differing traits. (CG1) In other words, a more specific problem occurs.

CP3. Is Mendel's observation and law concerning a pair of differing traits confirmable?

In addition, Correns also adopts Mendel's terminology to distinguish a pair of traits in terms of "dominating/recessive". It is worth noting that Correns attributes the terms "dominating" and "recessive" implicitly to the kinds of anlagen.

By undertaking the crossing experiments on peas differing in the colour of embryos (CE1) through six generations, Correns confirms Mendel's observation (1865) as follows.

1. In the first generation, all hybrid individuals are uniform and only the dominant trait (i.e. yellow in this case) appears.
2. When these seeds with yellow embryos are sown, plants are obtained, whose pods, which were produced by self-fertilisation, contain seeds with yellow embryos and seeds with green embryos. On the average, there are three yellow ones for each green one.
3. When the seeds with a green embryo, obtained in the F2 generation, are sown, plants are obtained, whose pods, which were produced by self-fertilisation, contain only seeds with green embryos, (the F3 generation). These, in turn, produce only

seeds with green embryos, (the F4 generation), etc. With respect to this trait, the recessive one, they behave like the pure variety, which carries it.

4. If the seeds with yellow embryo, obtained in the F2 generation, are sown, plants are produced which may be grouped into two classes, Class A, those plants, whose pods, which were obtained by self-fertilization, contain only seeds with yellow embryos (the F3 generation) and Class B, these plants, whose pods, which were produced by self-fertilization, contain seeds with yellow as well as seeds with green embryos (the F3 generation). Numerically, there are again on the average three seeds with yellow embryos for each one with a green embryo, just as in the F2 generation. The number of individuals in classes A and B is approximately one to two.

Moreover, embryos of Class A do not differ in their appearance in any way from those in Class B, only after the pods, which were produced by self-fertilization, have been harvested, can it be decided to which one of the classes the seed belonged.

5. Seeds with yellow embryos, which descended from plants of Class A (paragraph 4), produce plants, whose pods, which originated by self-fertilization, again contain only seeds with yellow embryos (the fourth generation). Plants, which develop from them in turn produce only seeds with yellow embryos etc. As regards this character, the dominant one, they behave like the pure variety, which carries it.

6. The seeds with green embryos, which are obtained from plants of Class B (paragraph 4, B) produce plants, whose pods, which originated by self-fertilisation again contain only seeds with green embryos (the fourth generation). Plants which develop from them in turn produce only seeds with green embryos, (the fifth generation) etc.; — just as did the green embryos of the second generation (paragraph 3).

7. The seeds with yellow embryos, which are obtained from plants of Class B (paragraph 4, B) again produce, just as it was described in paragraph 4, two types of plants, in the ratio one to two, whose seeds behave in the same way as described in paragraphs 5 and 6 and so forth.

Thus, it is evident that Mendel's 1 : 2 : 1 ratio in the progeny of pea plants with the

hybrid form was also observed and confirmed by Correns. In order to explain this phenomenon, Correns propose a hypothesis

CH1. In the fusion of the reproductive nuclei, the anlage for the recessive trait is suppressed by the one for the dominating trait. Prior to the definitive formation of the reproductive nuclei a complete separation of the two anlagen occurs, so that one half of the reproductive nuclei receive the anlage for the recessive trait, the other half the anlage for the dominating trait.

By applying CH1, Correns predicts the phenomena described by Mendel's LCT. Thus, Mendel's LCT is also confirmed, and CP3 is assertively answered.

Correns specifies CP2 into another problem.

CP4. Is Mendel's observation and law concerning two or more pair of differing traits confirmable?

More precisely, Correns' problem is

CP4'. Is Mendel's LCD confirmable?

According to Mendel's LCD, Correns predicts that there are four morphologically distinct classes of the combination of traits among the seeds in F2 generation, and the ratio of these classes should be in a ratio of 9 : 3 : 3 : 1. Correns accept Mendel's idealisation of the ratio of 315 : 101 : 108 : 32 into the ratio of 9 : 3 : 3 : 1. Moreover, the actual ratio obtained from Correns' experiments on maize (CE2) is 308 : 104 : 96 : 37. Correns idealises the actual ratio into the ratio of 9 : 3 : 3 : 1, and concludes that Mendel's LCD is well confirmed. Hence, Correns solves the CP4'.

Finally, Correns specifies CP2 into a third question.

CP5. Is Mendel's LCC universally applicable?

In fact what Correns was discussing is a reformulated version of Mendel's LCC.

CH2. In the hybrid, reproductive cells are produced in which the anlagen for the individual parental characteristics are contained in all possible combinations, but

both anlagen for the same pair of traits are never combination. Each combination occurs with approximately the same frequency.

The universality of CH2 is doubted by Correns. Correns suggests that there are constraints of applying CH2. Firstly, it only applies to the plants with pairs of differing traits where one member of a pair of traits dominates. Secondly, it may be only applicable to hybrids between varieties. These doubts are confirmed by Correns' observations on his experiments. For example, by crossing *Erfuter Folgerebse* (with colourless seed coat) with *Kneifelerbse* (with orange-red seed coat), or *Pahlerbse* (with orange-red seed coat), the seed coats within the same pod, obtained in the F1 generation, are sometimes colourless, sometimes intensely red, but usually orange with purplish-black spots. In other words, none of the traits can be regarded as the dominating trait. Moreover, in the F2 generation, the seeds obtained would display many transitional forms between two parental traits (i.e. colourless and orange-red). Therefore, Correns concludes that CH2 is not universally applicable.

Thus, Correns' exemplar on Mendel's study of *Pisum* can be summarised.

Table 17

Correns' Exemplary Practice on <i>Mendel's Study of Pisum</i>					
Research Problems	Vocabulary	Practical Guides	Hypotheses	Experiments	Patterns of Reasoning
CP1 CP2 CP3 CP4 CP4' CP5	Anlage Dominating trait (A) Recessive trait (a) Dominating Anlage Recessive Anlage	CG1	CH1 CH2	CE1 CE2	H-D confirmation

5.4 The Road to 1900: Mendel's Legacy

From a close reading of Mendel's, de Vries', Correns', Tschermak's, and Bateson's writings, I recognise that some constituents of Mendel's exemplary practice are preserved (or preserved with minor modifications) and passed on in the successors' exemplary practices, despite their different initial research problems. For example, Mendel's practical guide (MG3) that planting peas both in the field and in the pots indoors to protect plants from the foreign contamination is adopted by Tschermak.

The plants grew in pots in a closed room under the most uniform conditions possible. In the year 1899, competing plants from seeds of equal weight were also grown in pots in a covered place. Concurrently, parallel experiments were also made by growing plants in the open. (Tschermak, 1900b, p. 233, 1950, p. 43)

Some preserved constituents are not very surprising, but some are really Mendelian. In this section, I shall at first examine Mendel's legacy for the origin of genetics on the basis of my exemplar-based analysis. Then I shall propose an exemplar-based analysis of the origin of genetics.

Mendel's Legacy 1: The Focus on a Pair of Differing Traits

Some (for example, Müller-Wille & Orel, 2007; Olby, 1997) have already pointed out that one of Mendel's important achievements is that his approach to the study of the problem of development by focusing on the paired traits in the successive generations (MP1→MP2). Mendel's important observations and hypotheses are all about paired traits of hybrids and their progeny. As Müller-Wille and Orel's point out, "Mendel's focus on character pairs was not only an important methodological step, but had immediate consequences for his theorizing." (Müller-Wille & Orel, 2007, p. 211) The significance of Mendel's problem-specification (MP1→MP2) is also reflected in its reception at the beginning of the twentieth century. Although de Vries, Correns, Tschermak, and Bateson were not studying hybrid development, all of them adopted Mendel's approach to concentrate on paired traits. It is no surprise that de Vries' problem-specification (DP1→DP2) was indebted to Mendel's problem-specification (MP1→MP2).

In every crossing experiment only a single character or a definite number of them is to be taken into consideration... for experimental purposes the simplest conditions are presented by hybrids whose parents differ from each other in one trait only. (de Vries, 1900a, p. 84, 1966, p. 108)

Tschermak also adopted the Mendelian problem-specification to study his research problem.

The purpose was to study the immediate influence of the foreign pollen upon the constitution (form and color) of the seeds thus produced, and also to follow, in the next generation of hybrids, the inheritance of the constant, differentiating characters of the parental types used in the hybridization. (Tschermak, 1900b, p. 232, 1950, pp. 42–43)

In particular, Bateson is explicit on the point that a significant lesson learnt from Mendel in the study of heredity is that of focusing on differing traits.

[T]he subjects of experiment should be chosen in such a way as to bring the laws of heredity to a real test. For this purpose the first essential is that the differentiating characters should be few, and that all avoidable complications should be got rid of. Each experiment should be reduced to its simplest possible limits... [I]t is certain that by similar treatment our knowledge of heredity may be rapidly extended. (Bateson, 1902, p. 16)

As I have argued in the previous section, what de Vries, Correns, and Bateson in fact learnt from Mendel here is a way of refining a general problem into a more specific one. Despite beginning with different initial research problems, de Vries, Correns and Bateson, influenced by Mendel's work (1865), all find that refining their initial problems into a better defined and more narrowly scoped problem on paired traits is helpful in the further investigation.

Mendel's Legacy 2: The Conceptions of Dominating and Recessive and their Statistical Relations

Another legacy from Mendel's work is his use of the term "dominating" and "recessive" to conceptualise the paired traits and analyse the statistical relation of

them. Though the phenomenon of dominance had been observed by many (for example, Goss, 1824; Knight, 1799; Seton, 1824) by the first half of the nineteenth century, Mendel was the first to conceptualise the phenomenon in terms of “dominance” and “recessiveness”, and record and analyse the statistical relation of “dominating” and “recessive” traits. Mendel’s terminology was important for his work in the sense that it lay down the conceptual foundation for his analysis of data, recognition of the statistical regularity (e.g. the 3 : 1 ratio) and proposal of the hypotheses. It should be highlighted that the significance of Mendel’s terminology and his statistical analysis are intertwined. The statistical analysis cannot be made without the terms “dominating” and “recessive”, while the introduction to the conceptions of “dominance” and “recessiveness” is not interesting if no statistical regularity is obtained.

As I have shown, Mendel’s terminology was not only important for his work on the development of hybrids, but also enlightened the study of heredity around 1900. The terms “dominating” and “recessive” were adopted by de Vries, Correns, Tschermak, and Bateson, though their usages are different from Mendel’s in some aspects (for a summary, see Table 18). Correspondingly, the statistical analysis of the dominating and recessive traits was also introduced into the study of heredity, especially by de Vries and Bateson.

Table 18

	Dominating/Recessive
Morphological Traits	Mendel, de Vries, Correns, Tschermak, Bateson
Morphological Traits with a Certain Behaviour in the Progeny	Mendel
Hereditary Characteristics	De Vries
Hereditary Material	Correns, Bateson

I have to emphasise that the conceptions of dominance and recessiveness are important in the origin of genetics because they are useful in conceptualisation, hypothesisation, and idealisation rather than because they are essential conceptual

components, which are invariantly shared by both Mendel and the rediscoverers.

Mendel's Legacy 3: The Morphological-Cellular Correspondence

Among his laws, Mendel's LCC (MH3) was particularly important. In addition to illustrate the composition of seed and pollen cells in hybrids, it provides a "rather simple explanation" of "the most difficult [problem] in hybrid production": the problem of transformation of species. What is really novel in Mendel's LCC is the correspondence of the statistical relations of morphological traits and of germinal and pollen cells. It is worth noting that correspondence is a weaker notion than determination. Mendel never used the notion of determination, or causation in the LCC. Nevertheless, the morphological-cellular correspondence proposed by Mendel became a key to advance the study of heredity three decades later.

As I have mentioned, the biggest difficulty identified by Bateson (1902) in the study of heredity at the turn of the twentieth century was the lack of a reliable approach to study the physical basis of heredity. In fact there were a few theories of heredity concerning the physical basis. Weismann's theory of germ-plasm (1892) and de Vries' theory of pangenesis (1889) are two representative ones. Each proposes a conception of the physical basis of heredity. For Weismann, a biophore is a special particle in the cell as the determinant of a morphological trait, while for de Vries, a pangen is the fundamental unit, carrying a hereditary characteristics. However, neither provided a feasible way to test the hypothesis. In particular, the relation of visible characters and invisible "physical basis of heredity" is untestable experimentally. The state of art of the study of heredity by 1902 is, as Bateson neatly summarises, "[n]o one has yet any suggestion, working hypothesis, or mental picture that has thus far helped in the slightest degree to penetrate beyond what we see." (Bateson, 1902, p. 3)

In 1900, de Vries adopted and revised Mendel's morphological-cellular correspondence to support his theory of pangenesis, though he was never brave enough to formulate the law of segregation (DH2, DH3, DH5) as a trait-pangen correspondence (or determination) explicitly. In addition, de Vries also limited the application of his trait-characteristics correspondence in the case of true hybrids. Correns made "a significant step beyond Mendel" by reformulating Mendel's

morphological-cellular correspondence as a trait-anlage correspondence (CH1, CH2), though he was not clear on the implication of this reformulation in the study of heredity. Bateson was the first to make a sophisticated attempt to incorporate Mendel's morphological-cellular correspondence with the study of heredity. Firstly, Bateson reformulated Mendel's correspondence as a trait-paired allele determination. It is determination rather than correspondence, because Bateson explicitly talked of "the bearers of the character". Secondly, in contrast to the limited applicability of Mendel's correspondence, Bateson's trait-paired alleles determination is applicable broadly in certain phenomena of alternative inheritance. Though Mendel's morphological-cellular correspondence was not adopted without modification in de Vries', Correns', and Bateson's work, it was really helpful to set out an approach to work on the "inward and essential nature" of heredity.

Mendel's Legacy 4: Mathematical Representation and Manipulation

Another lasting legacy of Mendel's to the study of heredity in 1900 is his mathematical approach. Mendel denotes the dominating (constant) trait A, the hybrid trait Aa, the recessive (constant) trait a, and the distribution of these traits in the F₂ generation (A + 2Aa + a). All these symbolic notations are much more important and useful than thought. All Mendel's three laws can be formulated in terms of these notations.

$$\text{LDT: } A + 2Aa + a$$

$$\text{LCT: } (A + 2Aa + a)(B + 2Bb + b) = AB + Ab + aB + 2ABb + 2aBb + 2AaB + 2AaB + 4AaBb$$

$$\text{LCC: } \frac{A'}{A'} + \frac{A'}{a'} + \frac{A'}{a'} + \frac{a'}{a'} = A + 2Aa + a$$

Moreover, as we can see in the section 5.1, Mendel's LCT and LCC are introduced and articulated with the help of these notations and the mathematical manipulation of these. Mendel's mathematical notation was also adopted and further developed by de Vries. The distribution of characteristics in the F₂ generation is formulated by de Vries as $d^2 + 2dr + r^2$. The move from $A + 2Aa + a$ to $d^2 + 2dr + r^2$ was a breakthrough in the history of genetics. The equation $(d + r)(d + r) = d^2 + 2dr + r^2$ implicitly suggests the phenomena of the separation of hereditary

characteristics within pollen grains and ovules. This lays down the cornerstone for a later conception of particulate inheritance. The Mendel's laws and concepts "allelomorph" (Bateson, 1902, 1909), "factor" (Morgan et al., 1915; R. C. Punnett, 1905), "gene" (Morgan, 1926) were all articulated with the help of similar notations. Although, as many have pointed out, Mendel himself never had the conception of pairs of hereditary elements determining the morphological trait, his mathematical approach still played an indispensable role in the founding of genetics as a school of scientific practice. Therefore, the focus on a pair of differing traits, the conceptions of dominating and recessive and their statistical relation, the morphological-cellular correspondence, and the mathematical approach are four main components of Mendel's legacy.

Mendel's Contribution and the Origin of Mendelian Genetics Revisited

Now it is the time to reinterpret Mendel's contribution. It would be now clear that the "typical" textbook interpretations are problematic:

Mendel's contribution was ... the basic Laws of Heredity... (Brown, 1989, p. 5)

From the results of these experiments, [Mendel] described two basic rules governing the inheritance of traits. Since the early part of the 1900s, researchers have wondered why Mendel was successful in discovering how traits are inherited when earlier scientists were unable to make this basic conclusion. (Atherly, Girton, & McDonald, 1999, p. 17)

Gregor Mendel... discovered the basic principles of genetics in the mid-nineteenth century... [H]e examined the inheritance of such clear-cut alternative traits in pea plants as purple versus white flowers or yellow versus green seeds. In so doing, he discovered why some of these traits disappeared in one generation and then reappeared in another. By rigorously analysing the patterns of transmission through generations, he inferred genetic laws that allowed him to make verifiable predictions about which traits would appear, disappear, and then reappear in which generations. (Hartwell et al., 2008, pp. 13–14)

In 1866 Gregor Mendel published the results of experiments in which he had investigated inheritance in garden peas. From these findings he discovered the existence of discrete hereditary elements and rules determining their transmission from parent to offspring. (Hartl, Freifelder, & Snyder, 1989, p. 7)

As a result of his research with pea plants, Mendel proposed ... a theory of particulate inheritance. A genetic determinant of a specific character is passed on from one generation to the next as a unit, without any blending of the units. This model explained many observations that could not be explained by blending inheritance. It also proved a very fruitful framework of further progress in understanding the mechanism of heredity. (Suzuki et al., 1981, p. 100)

There are two common mistakes in these interpretations. First of all, as I have shown in Chapter 3, Mendel's concern was with the development of hybrids in their progeny, so it is historically flawed to understand Mendel's contribution as the introduction to the law or theory of heredity. Secondly, as I have argued in the section 5.1, it is inadequate to take the theory-driven approach to analyse the origin of genetics, so taking Mendel's contribution to be the formulation of a theory is problematic.

Alternatively one might regard Mendel's contribution to the history of genetics as a discovery of the laws of hybrid development. From a historical viewpoint, this interpretation is better than the standard textbook interpretations. Mendel's concern was about hybrid development, and his work did make a substantial contribution. However, there are two main problems:

Firstly, it is controversial that Mendel's laws of hybrid development are laws of nature, from a philosopher's point of view. Among philosophers, there is no consensus on what is a law of nature¹²², but most philosophers would agree that

¹²² Nevertheless, there are two mainstream ways of understanding laws of nature¹²²: the regularity view (for example, Ayer, 1963; Goodman, 1983; Molnar, 1969) and the necessitarian view (for example, Armstrong, 1983; Dretske, 1977; Tooley, 1977). According to the minimal account of the regularity view, laws of nature are empirical regularities in the sense that it is a law that all Fs are Gs if and only if all Fs are Gs where no local terms are involved. According to a minimal account of the necessitarian view, laws are singular statements describing the

laws of nature must be spatiotemporally universal. Take the case of Mendel's LDT.

... [O]f the seeds formed by the hybrids with one pair of differing traits, one half again develop the hybrid form while the other half yield plants that remain constant and receive the dominating and the recessive character in equal shares. (Mendel, 1865, p. 17, 1966a, p. 15)

It is very clear that, as Mendel himself recognised, such a "law" is not universally true. Though it can be argued that Mendel's laws are in fact *ceteris paribus* laws, this move might not be very helpful. Yes, if we could well define the limit of Mendel's laws and put it into a *ceteris paribus* clause, Mendel's laws would look like a good case of *ceteris paribus* laws. However, given the non-universality of Mendel's laws (especially LCT), it seems dubious if Mendel's laws can be characterised as *ceteris paribus* laws, just like nobody would insist that all Roman emperors are male is a *ceteris paribus* law. Hence it is clear that Mendel's contribution would be better not understood as a discovery of the laws of nature, especially given the philosophical controversy on the definition of laws of nature.

Secondly, even if Mendel's laws can be legitimately accepted as laws of nature, Mendel's proposal of the laws of hybrid development is not an obvious contribution to the history of genetics. It is not obvious in what sense Mendel's laws of hybrid development are important to the history of genetics. Nor is clear what aspects of Mendel's laws played an important role in the history. In addition, as I have shown in Table 13, Mendel's influence is much more than his theoretical construction. The interpretation of Mendel's contribution as the discovery of laws of nature suggests the neglect of the other crucial elements from scientific practice. Thus, it is problematic to argue that Mendel's contribution to the history of genetics is his proposal of the laws of hybrid development.

Another potential interpretation is that Mendel's contribution is a discovery of some important facts of hybrid development. Unfortunately, this interpretation encounters a similar problem to the law-based interpretation. Mendel's discovery

relationships that exist between universals in the sense that it is a law that all Fs are Gs if and only if there is a relation of necessitation between the properties F-ness and G-ness such that all Fs are Gs. Clearly, both views agree on the universality of laws of nature.

of the facts of hybrid development also fails to make an obvious contribution to the history of genetics. Moreover, facts can never be discovered without a proper representation. As Peter Bowler puts it, "Facts only appear as facts within an appropriate conceptual scheme." (Bowler, 1989, p. 6) Such an understanding overlooks Mendel's conceptual contribution to the history of genetics by introducing a vocabulary to describe and explain the phenomena. As Curt Stein indicates,

[Mendel's paper "Experiments on Plant Hybrids"] does not simply announce the discovery of important facts by new methods of observation and experiment. Rather is an act of highest creativity, it presents these facts in a conceptual scheme which gives them general meaning. (C. Stern & Sherwood, 1966, p. v)

Thus, Mendel's contribution is more than the discovery of some facts of hybrid development.

In contrast to all these interpretations, I argue that Mendel's contribution to the history of genetics is an exemplary practice of the development of pea hybrids in their progeny. More specifically, *Mendel introduced a set of contextually well-defined research problems on the development of hybrids in their progeny and the corresponding solutions, and some components of his exemplary practice greatly inspired and influenced de Vries', Correns', Tschermak', and Bateson's work, and lay down the cornerstone for the study of heredity in the 20th century.* In particular, as I have argued earlier in this section, Mendel's focus on a pair of differing traits, the conceptions of dominating and recessive and their statistical relation, the morphological-cellular correspondence, and his mathematical approach made an enormous impact on de Vries' and Bateson's work on heredity. Similarly, *de Vries', Correns', and Bateson's contribution can also be characterised as the exemplary practices, which also inspired and influenced the successors' work* (for example, Castle & Allen, 1903; Castle, 1903; Hurst, 1906; R. C. Punnett, 1905; Raynor & Doncaster, 1905) on heredity in the first decade of the 20th century. Therefore, the origin of genetics from Mendel to Bateson, I argue, can be characterised as a chain of exemplary practices.

In the origin of genetics, the earlier exemplary practices are accepted and learnt by the successor practitioners. It should be noted that to say that the practitioners accept an exemplary practice does not mean that all the components of that exemplary practice are accepted and shared dogmatically. Instead what is accepted and shared by all practitioners is the way of defining the problems and of solving these problems. In the case of the origin of genetics, what de Vries, Correns, Tschermak, and Bateson all shared and accepted is Mendel's problem-defining and problem-solving. Nevertheless, they still differed in how to understand the components of Mendel's exemplary practice and how to use them (or some of them) to solve their problems. For the "rediscoverers", Mendel's conceptualisation, hypothesisation, experimentation, and reasoning are just tools to solve Mendel's problems. And some of these are also useful to their own research problems. Thus, Mendel's vocabulary, hypotheses, practical guides, experiments and patterns of reasoning are accepted as tools to solve Mendel's problem of hybrid development in their progeny and their implication to solve successors' problems. The rediscoverers' acceptance of Mendel's exemplary practice is mainly due to the instrumental or pragmatic reason. In addition, to say that the exemplary practices are accepted does not mean that they are accepted invariantly by all the late practitioners. For example, it would be plausible to argue that de Vries and Bateson accepted and worked on the basis of Mendel's exemplar practice, while Hurst and Punnett accepted and worked on the basis of Bateson's exemplary practice rather than Mendel's. This is why I argue that the origin of genetics is better characterised as a chain of exemplary practices rather than a set of exemplary practices.

To some extent, characterising Mendel's contribution as the introduction to new problems and their solutions is not a completely new idea. In particular, the significance of Mendel's introduction of new research problems had been highlighted by many historians (For example, Bowler, 1989; Sandler & Sandler, 1985). In particular, Iris Sandler and Laurence Sandler explicitly pointed out:

Mendel ... defined his problem in purely genetic terms, and produced a correct and amazingly complete answer. (Sandler & Sandler, 1985, p. 69)

However, one crucial difference between Sandler's and my interpretation is that I

do not think that Mendel's work can be understood as a study of heredity. Sandlers fail to recognise that Mendel's study was in fact about hybrid development rather than heredity in general, and the problem of hybrid development cannot be conflated with of heredity. In addition, Sandlers' focus is mainly historical. Little is said about what the problem is and what the answer is, or how the problem and its solution influence the successor's work methodologically, conceptually, theoretically, etc.

Before finishing this section, I have to emphasise that the origin of genetics from Mendel to Bateson discussed in this thesis is definitely not a complete and comprehensive picture of the origin of genetics. As the title of Olby's book *Origins of Mendelism* has suggested, there are multiple origins of genetics. What I focus on here is only one path to genetics, as the subtitle of my thesis indicates. More precisely speaking, my task is to explore a new philosophical way to analyse and understand the development from Mendel's (1865), de Vries' (1900a, 1900c, 1900d), Correns' (1900), Tschermak's (1900a, 1900b) to Bateson's work (1902). To sum up, so far I have argued that Mendel's contribution can be characterised as an introduction to new research problems and their corresponding solutions. The origin of genetics from Mendel to Bateson is accordingly understood as a chain of exemplary practices.

5.5 Reconsidering the Problem of Long Neglect

In addition to provide an alternative way to characterise the origin of genetics, I shall argue that my exemplar-based analysis of the origin of genetics sheds light on a long-debated puzzle among historians of genetics, namely, the problem of the long neglect of Mendel's paper. In this section, I shall first review the problem of long neglect and its responses. Then I shall take the exemplar-based approach to showing that why Mendel's work was neglected by those who studied the problem of heredity in the 19th century is a pseudo-problem.

The Problem of Long Neglect

Given the vital role of Mendel's paper in the history of genetics, it has been a persistent puzzle: Why was the significance of Mendel's work not recognised earlier? In general, the explanations fall into two main groups. The first is that the significance of Mendel's work was not recognised earlier simply because his contemporaries did not accept it. The second is that the long neglect of Mendel's work was due to the fact that it was largely unknown to his contemporaries, especially those of importance. In addition, there is a third solution: The problem of long neglect is a pseudoproblem. Mendel's work was neither unaccepted nor unknown in his time. From the eyes of Mendel's contemporaries, Mendel's was hardly revolutionary at all. In the following, I shall first examine these old responses to the problem, and then propose a new solution on the basis of my exemplar-based analysis.

Old Response 1: Mendel's Work was Not Accepted

For a long time, Hugo Iltis's explanation (1932) had been the "standard" answer to the problem of long neglect. Iltis argues that during the mid-nineteenth century the time was not ripening for understanding Mendel's work. But finally at the turn of the twentieth century, "his time has come".

[T]he study of the cell nucleus during the closing decades of the nineteenth century, thanks to which the chromosomes had come to be recognised as the bearers of heredity, while the reduction division had been observed and its purpose understood, and fertilisation (amphimixis) had been recognised

as one of the most important causes of variability; Johannsen's experiments, and this investigator's vivid formulation of "population" and "pure line," of "phenotype" and "genotype"; de Vries' discovery of mutation, and the conception he based upon the mutation theory that a species is a mosaic of characters. Thanks to these converging trends, by 1900 the scientific situation was such that experiments of the kind performed thirty-five years earlier by Mendel had become absolutely essential to the testing of the various theoretical views. (Iltis, 1932, pp. 301–302)

In short, for Iltis, Mendel's work was ahead of his time. The significance of Mendel's work was not recognisable until the further development in the fields like cytology and heredity. This explanation had been widely accepted. Similar views were also held.

Mendel had produced a key piece for the jigsaw of biological theory – a much more important piece than he could have realized – but it was of no general use until the picture was sufficiently complete for it to be fitted in. (Gasking, 1959, p. 77)

One may say that the criterion of prematurity¹²³, as defined by Stent, without question applies well to the class cases of neglect of the work of Mendel... (Glass, 1974, p. 110)

It is clear that "ahead of his time" cannot be the one and only one explanation of why Mendel's work was not accepted by his contemporaries. In addition, the lack of generality of Mendel's laws is another explanation. I have shown that even Mendel himself well realised that his laws were not universally applicable. Thus, some historians regarded this as a key factor of the lack of success of Mendel's work.

Although Mendel's theory in fact ordered a mass of existing empirical knowledge, its application to this was not immediately and easily apparent.

¹²³ In his article "Prematurity and Uniqueness in Scientific Discovery", Gunther Stent provides a criterion of the prematurity of a scientific discovery to explain its failure to make an impact in its time: "A discovery is premature if its implications cannot be connected by a series of simple logical steps to canonical, or generally accepted, knowledge." (Stent, 1972, p. 84)

The theory must have seemed to have no other evidence in its favour than that collected by Mendel himself. (Wilkie, 1962, p. 5)

The analysis also suggests strongly that another criterion should be added to the determinative process, that of a lack of generality. Mendel's peas were thought to be unsuitable material for studying the heredity of species difference, and his laws were not clearly applicable to the other plants he attempted to use. (Glass, 1974, p. 110)

Mendel's mathematical approach is also regarded as an obstacle for his contemporaries to understand and appreciate his work.

[Mendel] was really a physicist, and brought to one of the great problems of biology the attitude of mind and the quantitative method of attack which had been in use for some time by physicists and by astronomers, and which was just coming to be used more widely by chemists. It was an unknown language to biology, though it fulfilled the essential requirements of scientific research better than anything which had gone before; and it came to biology at a time when those who were endeavouring to investigate inheritance by means of hybridization were not prepared for their task. (East, 1923, p. 232)

Mendel's mathematical treatment of his botanical data must have seemed strange in that time, when quantitative biology was unheard of. (Dodson, 1955, p. 194)

[B]iology was not ready for mathematical treatment. (Weinstein, 1962, p. 999)

In addition to his mathematical approach, Mendel's concern seems to have been removed from the interests of both biologists and breeders at his time. In other words, Mendel's work was thought to be irrelevant to the central problems in breeding studies (and biology more generally) in the 19th century.

Mendel's contemporaries therefore tended, either to misinterpret his work as a confused attempt to investigate the nature of species, or else to dismiss

it as being irrelevant to their own crucial problem of the origin of species.
(Gasking, 1959, p. 61)

[A] more general reason for the neglect of Mendel's work... that Mendel's contemporaries were unable to see the importance of his ideas because these ideas did not seem to them have any relevance to the problem of the nature and origin of species, which at that time appeared to be the central problem of biology. (Wilkie, 1962, p. 5)

This explanation was reinforced by Sandler and Sandler (1985). As I have mentioned in the section 5.3, they provide another interpretation of "Mendel's contemporaries failed to understand Mendel's work properly" by arguing that Mendel's usage of the term *Entwicklung* was so novel that no one fully understood it. At Mendel's time, there was no well-defined problem of inheritance of a morphological trait at all. The distinction between the problem of heredity and the problem of development was fuzzy. Most of Mendel's contemporaries (for example, Darwin) accepted a developmental model of heredity in which the transmission of morphological traits from one generation to the next and the process by which the morphological traits are produced in the growing organisms are just different stages of the same biological process. As Bowler put it, "[A] separate study of transmission was inconceivable." (Bowler, 1989, p. 6) It was Mendel who first explicitly defined the problem of heredity, the significance of which was not ever recognised. Thus, Mendel's work was not fully understood, and its significance failed to be appreciated until 1900.

Old Response 2: Mendel's Work was Unknown

Another popular solution to the problem of long neglect is to argue that Mendel's work was to a great extent unknown to most of his contemporaries. It has been argued that Mendel was an unknown monk and published a paper in a new and obscure journal at the time. Moreover, Mendel did not have any collaborators or students to follow his work. Even worse, some (for example, Mayr, 1982) have pointed out that Mendel's characteristic modesty prevented him from advertising his work to others. All these factors lead to the inaccessibility of Mendel's paper, and thus its silence.

In addition, Bateson suggests that another key factor of the inaccessibility of Mendel's work is that it was published at the wrong time when most of Mendel's contemporaries were distracted by Darwin's *Origin of Species*.

It is true that the journal in which [Mendel's paper] appeared is scarce, but his circumstance has seldom long delayed general recognition. The cause is unquestionably to be found in that neglect of the experimental study of the problem of Species which supervened on the general acceptance of the Darwinian doctrines. The problem of Species, as Kölreuter, Gärtner, Naudin, Wichura, and the other hybridists of the middle of the nineteenth century conceived it, attracted thenceforth no workers. (Bateson, 1902, p. 37)

Michael MacRoberts (1985) suggests another factor of the inaccessibility of Mendel's work. By comparing the fate of Mendel's paper on *Pisum* with the one on *Hieracium* on the one hand, and the informal communication network around these two papers on the other hand, he finds that the reception of Mendel's papers well confirms William Garvey and Belver Griffith's psychological study (1971) that most scientific communication takes place at the informal level. Therefore, MacRoberts argues that one significant explanation of the long neglect problem is that Mendel made so little informal communication.

Old Response 3: Mendel's Work was Nothing New

A third response to the problem of long neglect is to question the legitimacy of the question.

... [T]he problem of the long neglect of the Versuche is to a large extent a pseudo-problem. (Olby, 1979, p. 67)

The 'Great Neglect' is a product of historians of science, not of scientific history. (Callender, 1988, p. 72)

Both Olby and Brannigan argue that Mendel's paper was well within the hybridist tradition, and his work was not really revolutionary in this context. Based on Zirkle's research (1951), Brannigan (1979) concludes that "Mendel was not an obscure historical figure, long neglected for three and a half decades.

Nor was Mendel entirely accurately read by those who were most familiar with his work” because his important observations and “novel” approach were “recorded” and “pioneered” by his predecessors and contemporaries!

On the other hand, Callender argues that the anti-Darwinian implication of Mendel’s work sufficiently “accounts for the failure of his theories to make any significant impression on serious scientific opinion of his time,” especially given that both Alexander Makowsky, a leading member of the Natural History Society of Brünn who also presented in the same conference where Mendel presented his paper on *Pisum*, and Nägeli, the only known correspondence with Mendel on his paper, were supporters of Darwinism.

The Explanations of the Long Neglect of Mendel’s Paper	
Explanation	Further Explanation
Mendel’s work was not accepted by his contemporaries.	Ahead of his time / Prematurity (Gasking, 1959; Glass, 1974; Iltis, 1932; Zirkle, 1964)
	Lack of generality (Glass, 1974; Wilkie, 1962)
	Obscure application of mathematical models (Dodson, 1955; East, 1923; Gasking, 1959; Weinstein, 1962; Wilkie, 1962)
	Irrelevance to the central problems of his time (Gasking, 1959; Wilkie, 1962)
	Failure of comprehension (Gasking, 1959; Sandler & Sandler, 1985; Sorsby, 1965)
Mendel’s work was to a large extent unknown to his contemporaries.	Lack of informal communication (MacRoberts, 1985)
	Distraction by Darwin’s work (Bateson, 1902)
	Inaccessibility of Mendel’s paper (Dodson, 1955; Dorsey, 1944; Gasking, 1959; Mayr, 1982; Posner & Skutil, 1968)

The problem of long neglect is a pseudo-problem.	Anti-Darwinian Implication (Callender, 1988)
	Nothing Revolutionary (Brannigan, 1979; Olby, 1979)

The Re-examination of the Long Neglect

Despite many efforts of diagnosing the problem of long neglect, it still has yet to be well resolved. None of these explanations alone sufficiently accounts for the long neglect. It has been overwhelmingly discussed, so I do not intend to repeat the objections here. Rather, I intend to re-examine the problem of long neglect by analysing the problem first. The problem of the long neglect originates from the rediscovery event in 1900. Considering its great impact on the study of heredity, Bateson was puzzled by a fact that Mendel's work seemed to be forgotten for thirty-five years.

It may seem surprising that a work of such importance should so long have failed to find recognition and to become current in the world science.
(Bateson, 1902, p. 37)

It seemed to be natural for Bateson, as a first serious proponent of Mendelism, to have such a question. If Mendel's work was so important to the study of heredity, how could it be ignored or neglected for such a long time? Why was its significance not recognised earlier? However, this also reflects another fact. From the very beginning, the problem of long neglect is deeply rooted in a traditional understanding of Mendel's work: Mendel's work is about heredity. Because Mendel's work is about heredity, it must be puzzling why so many world-leading scientists like Darwin and Galton who made efforts to understand the phenomena failed to recognise the valuable implication of Mendel's work. This is also why Bateson's counterfactual fantasy had been so widespread among historians and biologists for a long time.

Had Mendel's work come into the hands of Darwin, it is not too much to say that the history of the development of evolutionary philosophy would have been very different from that which we have witnessed. (Bateson, 1902, p. 39)

If this is the logic of the problem of the long neglect, I argue that it is no longer a problem. Remember my argument that Mendel's concern was development of hybrids in their progeny, it is not surprising that his work was not warmly received by those who studied heredity in the 19th century. *What seems obvious to us was not obvious to Mendel's contemporaries, especially those who were particularly interested in the problem of heredity.* For most Mendel's contemporaries, a work on the development of pea hybrid would not obviously make a potential contribution to the study of heredity. The silence on Mendel's work before 1900 and also the struggle and confusion of understanding Mendel's work by de Vries, Correns, Tschermak, and many others in the first years of the twentieth century confirm my explanation. This reflects well the fact that Mendel's work on pea hybrid did not seem to be an obvious supplement to the study of heredity in the nineteenth century.

Nevertheless, my solution to the problem of long neglect based on the exemplar-based analysis should not be mistaken or conflated with the third solution I mentioned. Though I agree with Brannigan, Callender, and Olby on the point that to some extent the problem of long neglect is a pseudo-problem, I differ from them in why it is a pseudo-problem. Brannigan's solution is on the basis of Zirkle's research, in which Zirkle identifies five important discoveries (i.e. the principle of dominance, the principle of segregation, the 3 : 1 ratio, the perpetuation of these patterns over generations and the principle of independent assortment) in Mendel's work and dismiss them in terms of originality or novelty. For example, the phenomena of dominance and segregation, and the 3 : 1 ratio had been recorded by Mendel's predecessors. As I have mentioned, Zirkle and Brannigan are correct that the observation on the phenomenon of dominance was nothing new. In fact Mendel admitted that his observation on the phenomenon was merely a confirmation.

Experiments on ornamental plants undertaken in previous years had proven that, as a rule, hybrids do not represent the form exactly intermediate between the parental strains. (Mendel, 1865, p. 10, 1966a, p. 9)

However, I argue the 3 : 1 ratio was really a novel observation and

conceptualisation made by Mendel. Zirkle argues that Johann Dzierzon, a bee-breeder, already suggested the 3 : 1 ratio 11 years before Mendel's publication. In fact, in his publication in 1854, Dzierzon only wrote,

If [the queen] originates from a hybrid brood, it is impossible for her to produce pure drones, but she produces half Italian and half German drones, but strangely enough, not according to the type [not a half and half intermediate type] but according to number, as if it were difficult to fuse both species into a middle race. (Zirkle, 1951, p. 102)

On the basis of this passage, Zirkle boldly argues,

The genetic implication of this passage is obvious. Two types of drones being derived from unfertilized eggs means that two types of eggs were laid. If hybrid females produced two kinds of eggs in equal numbers, then the production by hybrid males of two types of sperms also in equal numbers is indicated by the internal logic of the situation. (This of course does not apply to bees for reasons which we need not mention here. A drone can produce only one kind of sperm.) Random fusion of such eggs and sperms could produce only a 1 : 2 : 1 ratio. In the presence of dominance, so well recorded by Knight, Sageret, Gärtner et al, this would appear as a 3 : 1 ratio. (Zirkle, 1951, p. 102)

Nevertheless, it is hardly a piece of evidence to show that Dzierzon recognised the 3 : 1 ratio. The 3 : 1 ratio was explicitly found nowhere in his paper, nor was it a natural implication that could have been easily made by Dzierzon or his reader. Zirkle's argument is definitely a 20th century reading of Dzierzon's paper. Thus, in contrast to Zirkle and Brannigan, I argue that the novelty of the 3 : 1 ratio in Mendel's work should not be dismissed. In addition, Callender's argument has gone too far. We have too little evidence to confirm or falsify Callender's conviction that Mendel was an opponent of descent with modification and his work was dismissed for his anti-Darwinian attitude. Therefore, my solution by applying the exemplar-based approach provides a new way out of the maze of long neglect.

Of course this should not be the end of the story of the exemplar-based analysis of

the problem of long neglect. There are still unsolved problems. Even if Mendel's work was not about heredity, it is undoubtful that Mendel's work on *Pisum* was still novel and interesting in both theoretical and methodological ways in the study of plant breeding. Why was the novelty and significance of Mendel's exemplary practice on *Pisum* overlooked in the 19th century? And, why was it adopted by de Vries, Correns, Tschermak, and Bateson at the turn of the 20th century? Although I would not be able to explore a comprehensive solution to these problems in this thesis here, I definitely contend that my exemplar-based approach also shed new lights on these issues. As I have indicated in the section 4.3, repeatability and usefulness are two intellectual characteristics of a good exemplary practice. The "rediscovery" of Mendel's work in 1900 is such a good example to illustrate this.

In 1900-1902, de Vries, Correns, Tschermak, and Bateson all acknowledged the usefulness of Mendel's exemplary practice to other research problems.

[T]he law of segregation of hybrids as discovered by Mendel for peas] has a basic significance for the study of the units of which the species character is composed. (de Vries, 1900a, p. 90, 1966, p. 117)

In order to explain the facts, one must assume (as did Mendel) that ... (Correns, 1900, p. 163, 1966, p. 125)

[Mendel's principle] proves to be of the highest significance for the study of inheritance in general. (Tschermak, 1900b, p. 235, 1950, p. 44)

[B]y the application of those [Mendelian] principles we are enabled to reach and deal in a comprehensive manner with phenomena of a fundamental nature, lying at the very root of all conceptions not merely of the physiology of reproduction and heredity, but even of the essential nature of living organisms, ... (Bateson, 1902, p. 35)

Moreover, all de Vries, Correns, Tschermak, and Bateson repeated Mendel's exemplary practice on *Pisum* in their own ways. Correns, as I have showed in the section 4.1, to a great extent repeated Mendel's experiments and hypothesisation to test his laws. In contrast, de Vries mainly repeated Mendel's conceptualisation and hypothesisation to reinterpret his old data, drawn from his massive

experiments on hybridisation in 1890s. Thus, it is not hasty to conclude that the repeatability and usefulness of Mendel's exemplary practice were recognised by de Vries, Correns, Tschermak, and Bateson at the turn of the 20th century. To some extent, it also explains why the significance of Mendel's work was well recognised in 1900 by these men. The failure of recognising the repeatability and usefulness (in particular) of Mendel's exemplary practice is one important intellectual explanation of why so many Mendel's contemporaries overlooked the significance of Mendel's work.

Summary

To sum up, in this chapter, I have proposed an exemplar-based characterisation of the origin of genetics from Mendel to Bateson. Furthermore, I also argued that my exemplar-based characterisation provides an alternative understanding of the development of the practice from Mendel to Bateson, which is not framed by theory, and offers a new way to re-examine the problem of long neglect.

6

Why Exemplars? A Defence and Further Articulation

In this chapter, I aim to defend my exemplar-based approach to analysing the origin of genetics. Firstly, I shall discuss and examine the potential responses to my objections from the theory-driven approach, and defend the superiority of the exemplar-based account of the origin of genetics to the theory-driven one. Secondly, I shall argue that my exemplar-based approach is better fit than a potential mechanism-based one to characterising the origin of genetics. Thirdly, I shall make some further notes on the exemplar-base approach in general.

6.1 The Potential Responses and Challenges from the Theory-Driven Approach

Potential Response 1: The Problem of Theory-Identification Revisited

One crucial problem that I identify for the theory-driven approach in the section 1.2 is the problem of theory-identification: If the origin of genetics is basically construed as a development of a theory of heredity, there is a difficulty of identifying that theory in history. There are two potential ways of defending the theory-driven account of the origin of genetics.

One way to defend the theory-driven approach is to argue that there is a theoretical consensus invariantly shared by Mendel, de Vries, Correns, Tschermak, and Bateson. It can be argued that the idea that there are two determinants for a heritable trait consisted in the “core” of the theory that was invariantly preserved in the practices of these scientists and distinguished theirs from other contemporaries working in the problem of heredity in the late 19th and early 20th century. The determinants can be loosely construed as the postulated factors, whether the factors are understood realistically or instrumentally. It is evident that the idea of two determinants for a heritable trait can be found in all of de Vries’, Correns’, and Bateson’s work, though not all explicitly formulated. For de Vries, a heritable trait is somehow dependent on the composition of two characteristics in the reproductive cell.

In the hybrid the two antagonistic [characteristics] lie next to each other as anlagen. In vegetative life only the dominating one is usually visible...

In the formation of pollen grains and ovules these [characteristics] separate....

If dominating is designated by d and recessive by r, fertilization yields:

$$(d + r)(d + r) = d^2 + 2dr + r^2$$

or

$$25\% d + 50\% dr + 25\% r$$

The individuals d and d² have only the dominating characteristics, those of r and r² constitution possess only the recessive the recessive characteristics, while the dr plants are obviously hybrids. (de Vries, 1900a, p. 86, 1966, pp. 111–112)

Correns suggested that a heritable trait is somehow dependent on two anlagen in the reproductive nuclei.

... [P]rior to the definitive formation of the reproductive nuclei a complete separation of the two anlagen occurs, so that one half of the reproductive nuclei receive the anlage for [one trait], the other half the [other]. (Correns, 1900, p. 166, 1966, p. 126)

For Bateson, a heritable trait is dependent on a pair of allelomorphs.

Each such character, which is capable of being dissociated or replaced by its contrary, must henceforth be conceived of as a distinct unit-character; and as we know that the several unit-characters are of such a nature that any one of them is capable of independently displacing or being displaced by one or more alternative characters taken singly, we may recognize this fact by naming such unit-characters allelomorphs. So far, we know very little of any allelomorphs existing otherwise than as pairs of contraries, but this is probably merely due to experimental limitations and the rudimentary state of our knowledge.

In one case (combs of fowls) we know three characters, pea comb, rose comb and single comb; of which pea and single, or rose and single, behave towards each other as a pair of allelomorphs, but of the behaviour of pea and rose towards each other we know as yet nothing. (Bateson, 1902, pp. 18–19)

Although Mendel never explicitly stated the idea that there are two determinants for a heritable trait, it can be argued that he implicitly suggested that a heritable trait is somehow dependent on a pair of cells with a kind.

[I]n an average of many cases it will always happen that every pollen form A and a will unite equally often with every germinal-cell form A and a; therefore, in fertilization, one of the two pollen cells A will meet a germinal cell a, and equally, one pollen cell a will become associated with a germinal cell A, the other with a.

... The striking phenomenon, that hybrids are able to produce, in addition to the two parental types, progeny that resemble themselves is thus explained: and both give the same association, Aa, ... Therefore

$$\frac{A}{A} + \frac{A}{a} + \frac{A}{a} + \frac{a}{a} = A + 2Aa + a \quad (\text{Mendel, 1865, pp. 29–30, 1966a, p. 30})$$

In contrast, no one else in the period 1865 - 1900 expressed a similar idea on two determinants for a heritable trait. For example, as an influential theory of heredity in the 19th century, Darwin's theory of pangenesis (1868) says little on the numerical relation of gemmules in the formation of a heritable trait. Therefore, the idea on the two determinants for a heritable trait is the characteristic component

of the theory of early Mendelian genetics. Thus, the problem of theory-identification is resolved. Moreover, given the idea of two determinants for a heritable trait as the theoretical consensus, the origin of genetics can still be characterised in a theory-driven way: Mendel proposed a theory in 1865. De Vries developed Mendel's theory by incorporating his theory of pangenesis. Correns tested Mendel's theory by conducting similar experiments and reformulated it in terms of anlagen. Bateson defended and further developed Mendel's theory on the basis of de Vries' and Correns' revision. Moreover, there is a development of the conception of determinant for a heritable trait, from Mendel's "kinds of cell", de Vries' "characteristics", Correns' "anlagen", to Bateson's "allelomorphs". The only price has to be paid in this defence is to exclude Tschermak's work from the origin of genetics.

However, I shall argue that this potential defence is unsuccessful. It is still problematic to argue that the idea that there are two determinants for a heritable trait was the theoretical consensus among Mendel, de Vries, Correns, Tschermak, and Bateson, though it seems that the idea was implicitly suggested in their works. Recall de Vries' statement that "In the hybrid the two antagonistic [characteristics] lie next to each other as anlagen. In vegetative life only the dominating one is usually visible". In addition to read this as a piece of evidence to support that de Vries had an idea on that two determinants for a heritable trait, one can use it to support that de Vries had an idea on one determinant for a heritable trait. This second interpretation seems to be better compatible with de Vries' theory of pangenesis (1889). As I have mentioned, for de Vries, every heritable characteristic has its special kind of pangen. When a pangen is in the active state, the corresponding heritable characteristic is visible. It is evident that in 1889 de Vries held the view that there is one pangen for one heritable trait, and it is more plausible to argue that his 1900 statement that "in vegetative life only the dominating [characteristic] is usually visible" suggests his belief on one determinant for a heritable trait rather than two. Thus, it is doubtful that de Vries had an explicit idea that there are two determinants on a heritable trait.

What is worse, a careful reading of Mendel's paper (1865) will show that Mendel did not have the idea that there are two determinants for a heritable trait. Firstly,

there are some texts which do not support that Mendel had the idea of paired determinants. Mendel, for example, (1865, p. 31, 1966a, p. 32) denotes the trait type of the combined kinds of cells $\frac{Ab}{ab}$ as Aab. If Mendel had had the idea that paired kinds of cells determines (or at least corresponds to) a heritable type, the trait type should have been Ab rather than Aab. Secondly, although Mendel (1865, p. 30, 1966a, p. 30) indicates that the cell type $\frac{A}{A}$ corresponds to the morphological trait A, $\frac{A}{a}$ to Aa, and $\frac{a}{a}$ to a, it should be noted that it is in fact the cell type A corresponds to the morphological trait A. When one pollen cell A becomes associated with the germinal cell A, the fertilised cell only has the cell type A. It is the cell type A rather than $\frac{A}{A}$ that corresponds to the morphological trait A. In other words, it is the cell type rather than a pair of cell types corresponds to a heritable trait. This is also why Mendel indicates that the cell type $\frac{Ab}{ab}$ corresponds to the trait type Aab rather than Ab. So, the speculation that Mendel had the idea of paired determinants is not well supported by Mendel's paper. Therefore, given the current evidence we have, it is insufficient to show that the idea that there are two determinants for a heritable consisted in the core of the theory, which was invariantly shared by Mendel, de Vries, Correns, and Bateson. Hence, the problem of theory-identification remains unsolved.

The other way to defend the theory-driven approach against the problem of identification is to take a pluralist stance by arguing that even if there was no well-formulated theoretical consensus in the origin of genetics, it is not a serious objection to the theory-driven approach. It seems possible to characterise and structure some discussion by reference to aspects of an underlying theory without actually identifying that underlying theory as a whole. Perhaps one could use the set of models instantiated by the theory, or similar. A practitioner of genetics in the early period could identify, say, the theory of genetics, and then move on to do some of these subsequent activities, without fully defining or characterising the entire underlying theory. In the case of the origin of genetics, it can be argued that despite theoretical variations of Mendel's, de Vries', Correns', Tschermak's, and Bateson's work, they all could be characterised as different versions of a theory. Thus, the origin of genetics can be characterised as a pluralistic development of a theory.

Unfortunately, this response is not tenable, either. If Mendel, de Vries, Correns, Tschermak, and Bateson are identified within a school of scientific practice centrally based on a theory, it is assumed that they share some theoretical components. There must be a theoretical consensus among them so as to identify them within in a school of scientific practice. The “theoretical consensus” here does not necessarily suggest a full-fledged theory of heredity. However, some theoretical components, like concepts or hypotheses, are necessarily accepted as the theoretical foundation for their practices. Otherwise it is arbitrary to examine Mendel’s, Mendel’s, de Vries’, Correns’, Tschermak’s, and Bateson’s work to study the origin of genetics. It is a task for anyone who takes the theory-driven approach to identify the theoretical consensus among Mendel, de Vries, Correns, Tschermak, and Bateson. It is also a task for anyone who takes the theory-driven approach to articulate the theoretical change (or progress) made by de Vries, Correns, Tschermak, and Bateson. After all, anyone who takes the theory-driven approach has to encounter the problem of identification. What is more, it should be noted that even if a pluralist response is successful, the defence of the theory-driven approach is not complete. As I have discussed in Chapter 1, there are four main problems. It is difficult to see how a pluralistic can overcome all the four problems.

To sum up, I have shown that firstly, the idea that there are two determinants for a heritable trait cannot be the core of the theory of heredity in the origin of genetics, and secondly, the problem of theory-identification is still an urgent question for those whom take the theory-driven approach to answer.

Potential Response 2: The Problem of Exemplar-Centrality?

Another problem that I identify for the theory-driven approach is the problem of theory-centrality, which is, the theory-driven approach assumes the centrality of the role of theory in the origin of genetics. Some might argue that the exemplar-based approach is vulnerable to a similar objection. The exemplar-based approach provides nothing really novel, compared with the theory-driven one. Those philosophers who take the theory-driven approach are accused of identifying an explanatory central theory when studying the history of genetics, while it appears to some that the exemplar-based approach suggests that the first task of

studying the history of genetics is to identify an exemplary practice. The shift from a theory to an exemplary practice does not seem to change too much. In response, I argue that the crucial difference is that according to the theory-driven account of the origin of genetics suggests that the practices of Mendel, de Vries, Correns, Tschermak, and Bateson were centred on a theory, while according to the exemplar-based account, the origin of genetics was characterised as a chain of exemplary practices. The exemplar-based approach does not warrant the central role of any exemplary practice in history. Nor were all of the practices in the early history of genetics centred on any exemplary practice.

Nevertheless, some may further argue that according to the theory-driven account, the origin of genetics can also be characterised as a chain of versions of a theory. No single version of a theory of heredity was regarded as the driving force for the practices in the origin of genetics. The theoretical changes of these different versions of the theory of genetics are detailed in Darden's analysis. In reply, I argue that, the problem of centrality is still there. Only if one characterises Mendel's, de Vries', Correns', Tschermak's, and Bateson's work as different versions of a theory, it still implicitly assumes a central theory. Therefore, the problem of theory-centrality remains. In contrast, the exemplary account does not privilege the centrality of any exemplary practice.

Moreover, there are two substantial differences between the theory-driven and exemplar-based approaches. Firstly, the exemplar-based approach provides a new unit of analysis in the history of genetics. The philosophers, who take the theory-driven approach, used to use theories, as the most popular unit of analysis, to characterise the history of genetics, or the practice of genetics. However, such an approach leads to a dream of a macro-unit, which can identify the practice of a scientific community by a set of common features. For instance, whether a scientist is part of a theory is to see if she makes a commitment to a set of theoretical components, which consist in the core of a theory. I call the unit of analysis like theory *macro* because it is assumed to be a compressive system or structure, which can capture the multifaceted nature of the practice of a scientific community. The macro unit suggests that there is a consensus, which consists in the fundamental component of the practice of a community and is invariantly shared by the

practitioners of a scientific community throughout the time.

However, this dream of a macro-unit is too utopian. There are two main difficulties of the search for a macro-unit. The first problem is about identification. As I have shown in 1.2, it is extremely difficult to determine the common features of the practice of a scientific community. Consider the explanatory aim of the theory. Though classical geneticists' work in 1910s can be characterised as a coherent set of epistemic activities aiming at explaining the phenomenon of transmission inheritance, there are some important works (e.g. Sturtevant's investigation on $C_{III B}$), which were undertaken without such an aim. Thus, it is a difficult task to identify some common features of the practice of a scientific community. In addition, a related problem is about investigative freedom. The macro-unit, I mean the notion of a theory, has the limitation to reflect the investigative freedom of scientists' practice. As we can see in the case of Sturtevant's investigation of the $C_{III B}$, even with the same ultimate aim, scientists in the actual practice often have other aims, while these practices cannot be excluded from the school of practice. If we take the theory-driven approach dogmatically, we have to bite the bullet by excluding Sturtevant's work from the practice of classical geneticists, which is highly implausible.

In comparison, an exemplar is not this kind of macro-unit. Rather it is a micro-unit. Unlike the macro-unit, the micro-unit is not assumed to be the fundamental component of the practice of a scientific community in the sense it is invariantly shared by the practitioners in history. However, a micro-unit suggests

Remember that an exemplar is a set of contextually co-defined research problems and their solutions. Though de Vries, Correns, Tschermak, and Bateson all accept Mendel's exemplary practice on *Pisum*, it does not mean that they all accept the concepts, methodologies, hypotheses themselves. Rather they accept the concepts, methodologies, and hypotheses as the tools to define and solve their own research problems. As I have argued in the section 5.4, there is no common feature of an exemplary practice shared invariantly by a scientific community throughout the history. Instead there is a chain of exemplary practices, in which successive exemplary practices are correlated with earlier ones via the reception, modification,

and application of some constituents. Thus, the practice of early genetics is not identified by any persistent common feature of a macro-unit (e.g. a theory). Rather, it is identified by a series of exemplary practices. Thus, it is in this sense that the exemplar is a micro-unit of analysis.

In addition, there is another crucial difference between the exemplar-based and the theory-driven approaches. The theory-driven approach is a descriptivistic approach in the sense that it assumes that a school of scientific practice can be identified by a consensus among practitioners, which can be summarised as a set of descriptive conditions. For example, the theory-driven approach relies on the theory-centric view which assumes the central role of a theory T in the practice of a scientific community. Thus, a school of scientific practice is identified by a set of descriptive conditions, which suffice to determine T . Such a descriptive approach encounters the problem of identification. When scrutinising the history of science, we have great difficulties of identifying such a set of descriptive conditions. In the case of the origin of genetics, it is extremely difficult to identify any theoretical consensus among Mendel, de Vries, Correns, Tschermak, and Bateson. The descriptivistic approach assumes too much. In addition, as I have shown in the section 1.3, such an analysis overlooks the role of investigative practice. Even if within a community of scientists with a definite aim, there are some practices which do not strictly follow the ultimate aim. Again, Sturtevant's investigation of the $C_{III}B$ is such a good example. Sturtevant is a leading figure in the Morgan school, but his work on $C_{III}B$ cannot be simply characterised as a practice centred on the theory of the gene or the discovery of the mechanism of transmission inheritance.

In comparison, the exemplar-based approach is a non-descriptivistic approach to analyse and understand the history of genetics. An established school of genetic practice is not identified by a set of descriptive conditions (e.g. explanatory aims or theoretical consensus). Rather it is characterised by a historically contingent series of exemplary practices. The series of exemplary practices cannot be reductively identified by an invariantly accepted set of descriptive conditions. The relation between any two successive exemplary practices is historically contingent. This is the second novel contribution of the exemplar-based approach, namely, the introduction to a non-descriptivistic approach to analysing the history of genetics

(especially the origin of genetics). Therefore, the exemplar-base analysis of the origin of genetics is not reducible to a theory-driven analysis. To sum up, the exemplar-based approach is exempt from the potential attack of the problem of centrality.

Challenge 1: Why are Exemplars better in any sense?

Still some may challenge the superiority of the exemplar-based approach to the theory-driven one. Even if the exemplar-based approach helps us have a plausible account of the origin of genetics, it just provides an alternative way to characterise the history of genetics. It is still too early to conclude that the exemplar-based approach is better fit than the theory-driven one in analysing the origin of genetics. In the following, I shall summarise the reasons for the superiority of the exemplar-based approach in analysing the origin of genetics.

Firstly, as I have argued earlier in this section, the exemplar-based approach is exempt from any kind of problem of identification. In contrast, the theory-driven account cannot overcome the problem of theory-identification. Secondly, the exemplar-based approach does not encounter a problem of centrality as the theory-driven one does. No single exemplary practice is assumed to play a central role in the practice throughout the history. Thirdly, the exemplar-based approach enables us to articulate more facets of the origin of genetics. The non-theoretical aspects of the practice and their relation to the theoretical ones have been investigated and highlighted in greater detail. Fourthly, the exemplar-based approach provides a new way to examine the puzzle of long neglect, which persistently puzzled those who take the theory-driven approach. Not only does the exemplar-based approach provide a new explanation of why those who were interested in the problem of heredity in 19th century failed to recognise the significance of Mendel's work, it but also offers a contrastive explanation of why it is that de Vries, Correns, Tschermak, and Bateson rather than Mendel's contemporaries who recognised the significance of Mendel's work by appealing to the characteristics of a good exemplary practice. Therefore, given the four reasons above, I am confident to conclude that the exemplar-based approach not only provides us a new way to analyse the origin of genetics, but also enables us to have

a better fit account.

6.2 A Mechanistic Salvage?

Some may wonder that even if the exemplar-based approach is better fit than the theory-driven one in analysing the origin of genetics, is there any other alternative way to analyse and characterise it? In this section, I shall attempt to explore a mechanistic analysis of the origin of genetics and compare it with the exemplar-based one.

Recently, Darden (2005, 2006b) develops an alternative way of analysing the biologists' practices in terms of seeking mechanisms. For Darden, "biologists often seek to discover mechanisms". (Darden, 2006b, p. 271) A mechanism is the explanans for a certain phenomenon. Darden's favourite characterisation of mechanisms is as follows.

Mechanisms are entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions. (Machamer, Darden, & Craver, 2000, p. 3)

The discovery of a mechanism is a piecemeal and incremental process with refinement *via* the practices of phenomena-characterisation, schema-construction, schema-evaluation, and schema-revision. The discovery begins with the characterisation of a certain phenomenon by precipitating conditions, inhibiting conditions, modulating conditions and so on to constrain the space of possible mechanisms for the phenomenon. The characterisation of a phenomenon is followed by the construction of a mechanism schema, a highly abstract representation for a mechanism, involving finding analogies in the history or contemporary practice of science, localising the phenomenon to a certain place (or level), or sketching hypothetical roles that components of the mechanism being sought are expected to carry out and work to specify them. Then the task is to look for the working entities and activities that play the roles in the abstract schema by filling the black boxes and grey boxes in the mechanism schema to produce a mechanism in which all the parts are glass boxes.

The evaluation of a mechanism may begin with a superficial schema which merely redescribes a phenomenon rather than explains it. Alternatively, the evaluation

begins with an incomplete sketch of components of the mechanism with black and grey boxes. The location and nature of the missing parts in a sketchy schema provides guidance as to what is to be sought by exploring an experimental setup. Or in other cases, the evaluation may also begin with conjecturing the possibility or plausibility of the work of a mechanism, or may be undertaken to compare with the rivals.

There are two main kinds of failures in the sketch of a mechanism schema: incompleteness and incorrectness. While the evaluation deals with the problem of incompleteness, the main task in the revision stage is to remove the incorrectness in mechanistic hypotheses when an evaluation strategy detects an anomaly, an empirical finding that provides evidence against a hypothesised mechanism. Anomaly resolution begins with an examination to ensure that the anomaly is not an observational or experimental error. Then a diagnosis of the anomaly is required. It is to be determined if the anomaly can be localised outside the domain of the mechanism schema, or if it results from an abnormality and thus is immune to the modification of the mechanism schema, or if the anomaly requires a splitting of the domain in which the mechanism was claimed to operate, or if it is a falsifying anomaly so that the entire proposed mechanism schema needs to be abandoned.¹²⁴

Thus, a mechanism-based approach can be proposed accordingly as follows:

In order to study the history of biology, first of all one has to characterise and identify the mechanism *M* that a community of scientists are/were working on. Then for *M*, one has to determine the working entities and activities, detail how they are discovered by filling the black boxes and grey boxes in the abstract schema, and examine how the mechanism schema is evaluated and revised.

Certainly this mechanism-based approach, compared to the theory-driven approach in analysing the history of biology, has several advantages. Firstly, many biologists do label their work as the discovery of mechanism. The term “mechanism”

¹²⁴ Note that the three stages of the discovery of a mechanism are not equally weighted in the actual practice. One can have weak practice of construction while one has good practices of evaluation and revision.

is not only widely used in the discourse of contemporary biological sciences, but also talked of in the history. The title of Morgan's book *The Mechanism of Mendelian Heredity* (1915) is a good example. Secondly, Darden's characterisation of the construction of a mechanism schema (e.g. filling the black boxes) well captures and reflects some characteristics of the actual practice of biologists. For example, the practice of the protein synthesis is convincingly characterised and explained by the mechanism-based approach.¹²⁵

But, what about the origin of genetics? By applying the mechanism-based approach, Darden (2005) characterises the history of Mendelian genetics as a process of the discovery of the mechanism of heredity. Accordingly, the origin of genetics can be characterised as a chain of early attempts to discover the mechanism of heredity as follows.¹²⁶ Mendel (1865) characterised the phenomenon of transmission in the case of *Pisum* by describing the 1:2:1 ratio among the offspring of peas hybrids and the independent behaviour of morphological traits in the transmission through generations. In addition, Mendel also constructed a mechanism schema within the hybridist framework by postulating the kinds of cell (the working entities) and their correspondence with morphological traits (the activities). Mendel's mechanism schema has two main problems: superficiality and incorrectness. Although it is useful to predict and describe the behaviour of the mechanism, Mendel's schema fails to explain explicitly how the internal components or the organisational and productive features by which the mechanism works. Secondly, Mendel's schema is incorrect in the sense that it was eventually shown that kinds of cell, as "determinants" of morphological traits, do not exist.

Based on Mendel's phenomenon-characterisation and schema-construction, de Vries (1900a, 1900c, 1900d) recharacterised the phenomenon in a wider scope (with data of more species) and reconstructed a mechanism schema within the

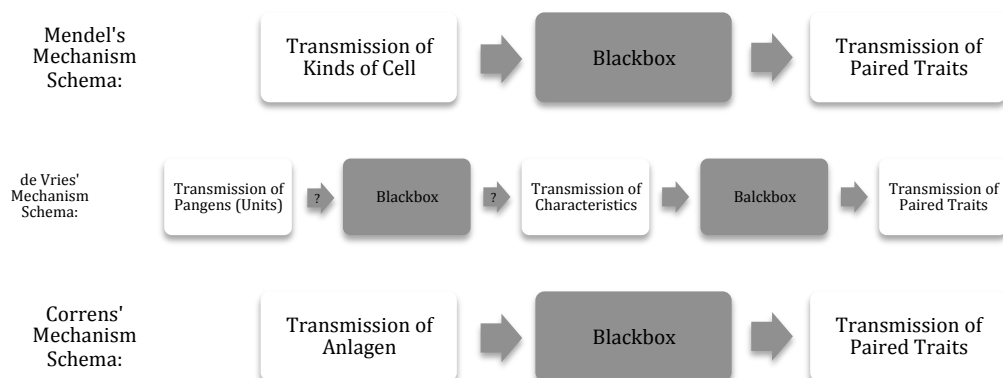
¹²⁵ For more detail, see Darden and Craver (2002).

¹²⁶ Darden did not provide a detailed articulation of the mechanism-based account of the origin of genetics. According to our conversation in ISHPSSB 2015 (Montreal, Canada), Darden contended that the first "mature" mechanism schema in the history of genetics was constructed by Morgan in 1910s. Her work on the discovery of mechanism of heredity concentrates on Morgan's and his colleagues' schema-construction since 1910s. Mendel's and early Mendelians' work are not taken into consideration. The mechanism-based account illustrated here is my attempt to take a mechanism-based approach based on my understanding of Darden's and Craver's work (Craver & Darden, 2013; Darden, 2005, 2006a).

framework of his work on pangenesis (1889). De Vries' schema is better than Mendel's with respect to completeness in the sense that de Vries' schema is more explicit on the behaviour of hereditary characteristics in the formation of pollen and ovules, which is a black box in Mendel's schema. Nevertheless, de Vries was still implicit on the activities of pangens (working entities) in his schema.

Following Mendel's phenomenon-characterisation, Correns (1900) revised Mendel's schema by specifying the working entities to be anlagen in the cell and their activities in the formation of the reproductive nuclei. Compared with Mendel's and de Vries' ones, Correns' schema is closer to Morgan's classical schema. In particular, Correns made a significant step forward in the localisation of the working entities of the mechanism of transmission heredity.

The significance of Bateson's book (1902) was, to a great extent, methodological. By the time Bateson had not begun his experimental work on testing the Mendelian approach in studying the problem of heredity. However, he still sketched an outline for the discovery of a mechanism of heredity. By identifying the problem¹²⁷, namely, how one can bridge the gap between the study of visible phenomenon of heredity and of physical basis of heredity, Bateson specified the blackboxes in the discovery of a mechanism. In addition, Bateson made a substantial revision of the mechanism schema by introducing new terminology on the basis of contemporary scientific knowledge. In particular, his usage of the conceptions "gamete", "zygote", and "allelomorph" reinforced Correns' localisation of the hereditary material within the cell. Therefore, the origin of genetics from Mendel to Bateson can be characterised as a series of attempts to discover the mechanism of heredity from 1850s to 1900s.



¹²⁷ For more detail, see section 4.3.



This mechanism-based analysis is attractive in some aspects. Firstly, most of the practice in the origin of genetics can be well characterised as the practice of the discovery of a mechanism. For example, both Mendel's and de Vries' work involved in characterising the phenomena, while Bateson's introduction of Mendel's work to the study of heredity is well characterised as the practice of black box-filling. Secondly, the mechanism-based approach captures and characterises the continuity underlying Mendel's, de Vries', Correns', and Bateson's work, related by recharacterising the phenomenon, refining the working entities and their activities. In particular, my interpretation that Correns aimed to test Mendel's work fits well with the characterisation that Correns' work can be understood as the evaluation of Mendel's schema. Thirdly, the conceptual development from Mendel's "kind of cell", de Vries' "characteristics", Correns' "anlage", to Bateson's "allelomorph" is well reflected in the characterisation of schema-construction.

Nevertheless, this mechanism-based characterisation of the origin of genetics is still problematic. Firstly, it is indeed controversial as to whether Mendel, de Vries, Correns, Tschermak, and Bateson worked on the same mechanism. As I have emphasised, though all of Mendel, de Vries, Correns, Tschermak, and Bateson made substantial contribution to the origin of genetics, they in fact differed from each other in the research problems they were working on. Of course it can be argued that they all tried to explain the same phenomena (e.g. the 1:2:1 ratio), but they characterised the same phenomena differently. Although Craver and Darden (2013, p. 52) recognise that "[t]o describe a phenomenon is to characterize it in the language of a given field", they say little on the implication of the different characterisations of the same phenomenon. If, as Craver and Darden maintain, the characterisation of a phenomenon *P* is crucial for the discovery of the mechanism of *P*, then it seems natural to postulate that different characterisations of *P* lead to the construction of the different mechanism schemas. Thus, it is difficult to maintain that Mendel, de Vries, Correns, Tschermak, and Bateson are searching for the same mechanism. Nor can their practices be simply characterised as working on the same mechanism schema. Recall my historical analysis. Although de Vries' and

Bateson's work can be characterised as the practice of seeking mechanisms of heredity, it is not obvious that they were working on the basis of the same mechanism schema. If de Vries had had any mechanism schema in mind in 1900, it must have been his own in terms of pangens. On the other hand, even in 1902 Bateson did not seem to have an explicit mechanism schema of heredity. The main task of his book (1902) was to defend a prospect of a Mendelian approach to study heredity against Weldon's criticisms. Therefore, even if de Vries', Tschermak', and Bateson's work can be understood as attempts to discover the mechanism of heredity, it is clear that they all have different mechanism schemas. It is more plausible to argue that de Vries initially constructed a mechanism schema with pangens as working entities in 1889, while Tschermak's schema was implicitly constructed with valency (*Werthigkeit*) as working entities. In other words, they are working on different mechanism schemas rather than the same mechanism schema. Thus, even if part of de Vries' work (1900a, 1900c, 1900d) is well characterised as the practice of black box-filling, it seems more convincing to argue that de Vries was filling the black boxes in his own schema (1889) rather than Mendel's. Moreover, if Mendel's work is better characterised as discovering a mechanism of hybrid development, while de Vries' as seeking a mechanism of heredity, the mechanism-based characterisation seems difficult to characterise the continuity or connection between Mendel's and de Vries' work. In addition, it remains unclear how Mendel's mechanism schema is incorporated into de Vries' mechanism schema. The relation and influence of different mechanism schemas are insufficiently articulated in Darden and Craver's work.

In comparison, my exemplar-based analysis is exempt from these challenges. The exemplar-based analysis does not assume that Mendel and his successors aimed to discover the same mechanism. The continuity underlying Mendel's and the rediscoverers' work is better characterised as the reception, modification and application of Mendel's problem-defining, conceptualisation, hypothesisation, experimentation, and reasoning in the exemplary practices. Thus, in the case of the origin of genetics, the exemplar-based approach is better fit to analysing and interpreting the actual scientific practice.

More generally, the mechanism-based approach has another serious problem. The

mechanism-based approach is, to a large extent, similar to the theory-driven approach. The theory-driven approach assumes the central role of theory in the scientific practice, while the mechanism-based one presupposes that the aim of practice is to discover a mechanism. Once a mechanism is identified, the rest of work is to formulate a good schema by construction, evaluation, and revision. Yes, the scientists, especially biologists, sometimes work in this way. However, it is often not the case in the actual practice of scientists. Obviously, the origin of genetics, as I have shown, cannot be simply understood in such a way. It is difficult to maintain that Mendel, de Vries, Correns, and Bateson all shared the same aim as searching for a mechanism of heredity. Therefore, the mechanism-based analysis faces the problem of mechanism-identification.

Thus, even more boldly, I shall argue that the mechanism-based approach is a variant of the theory-driven approach. Though this mechanism-based analysis of Mendelian genetics is theory-free, it is still “theory-driven”, where Waters (2004) broadly construes “theory” as “some explanatory practice”. Since the mechanism-based approach explicitly assumes that the history of Mendelian genetics is structured by the discovery of a hereditary mechanism (as a pattern of explanatory reasoning), and the practice of Mendelian genetics is organised around efforts to discover the hereditary mechanism, it is quite similar to what Waters refers to as theory-driven understanding¹²⁸. As I have shown, Craver and Darden’s approach (2013) starts with characterising a given phenomenon, and then explore the mechanism of that phenomenon by construction, evaluation, and revision. Hence, Darden’s mechanism-based approach evidently assumes a variant of theory-centric view where theory is broadly understood as the practice with certain explanatory aim (e.g. the practice of discovery of a mechanism). In other words, like the theory-driven one, the mechanism-based approach encounters another problem, namely, the problem of mechanism-centrality.

Moreover, when analysing the history of biology by taking the mechanism-based approach, one has to ask questions like: What is the mechanism of heredity? What are the working entities of the mechanism of heredity? These questions in fact

¹²⁸ For a detailed discussion on Waters’ summary, see section 1.3.

expect ultimately monistic answers, while the biologists' practice is definitely not so monistically oriented. In other words, the mechanism-based approach suggests an oversimplified understanding of the history of biology. Even within the framework of the discovery of a mechanism, some practices in history still cannot be well captured. Recall Sturtevant's investigation of $C_{III B}$ ¹²⁹. It is little controversial that Sturtevant, a leading figure of the Morgan school, was devoted to studying transmission inheritance. Thus, it is convincing to argue that his work on *Drosophila* can be characterised as the discovery of a mechanism of transmission inheritance. However, as Waters has shown, the ultimate goal of his experiments on $C_{III B}$ mapping was not to explain the inheritance, but to reveal information about basic biological processes. Sturtevant's investigation of $C_{III B}$ cannot be characterised as the construction, evaluation, or revision of the mechanism schema. Furthermore, many biological practices cannot be completely rendered as monistically oriented explanatory practices. The mechanism-based approach is vulnerable to Waters' criticism. It is highly problematic to characterise the practice of any biological school in terms of explaining certain phenomena.

Therefore, I conclude that the exemplar-based approach is better fit than the mechanism-base approach in analysing and understanding the history of genetics, especially the origin of genetics. However, I also have to note that the mechanism-based approach formalised in this section is definitely not the authoratative or unique account of the mechanism-based approach. Nor do I conclusively argue that my exemplar-based approach is better than any potential mechanism-based one. Rather, my exemplar-based approach is better fit than my formulation of a potential mechanism-based approach in this section to analysing the origin of genetics. Hopefully this is the starting point of analysing the origin of genetics in terms of mechanism-discovery. There is much more to do on the mechanism-based approach and its comparison with the exemplar-based one.

¹²⁹ For a more detailed introduction, see section 1.3.

6.3 Further Notes on the Exemplar-Based Approach

The Prospect of the Exemplar-Based Approach: Monism? Pluralism?

So far I have tried to argue for the superiority of taking the exemplar-based approach to analysing the origin of genetics. It is naturally to ask about the prospect of the exemplar-based approach. Is it universally applicable to the history of science in general? Or, is it only applicable to study the origin or early period of the history of biological sciences?

Although I have argued that my exemplar-based account of the origin of genetics is better fit with the history than the theory-driven and mechanism-based ones, it should be noted that I am not trying to argue that the exemplar-based approach is the only good approach to analysing the origin and history of a science. Nor do I venture to argue that the exemplar-based approach is better than all other alternatives here. Rather, I am pluralistic on the approaches to analysing and interpreting the history of a science. Though I contend that my exemplar-based account of the origin of genetics is better than the theory-driven and a potential mechanism-based ones, I am open to the possibility that other approaches might be better fit to analysing and interpreting a different period of the practice of genetics, or the origin of a different science.

Moreover, I believe that, to some extent, the exemplar-based approach and other approaches (e.g. the theory-driven and mechanism-based ones) are complementary to each other. On the one hand, the exemplar-based analysis can learn and benefit from the discussions on theory construction and mechanism discovery. Take the case of hypothesisation in an exemplary practice. As I have emphasised in 4.3, there is no universal account of hypothesisation. Rather the practice of hypothesisation in different exemplars should be analysed and characterised within its context. For example, in Mendel's case, his hypothesisation is best characterised as proposing hypothesising and confirming them by experiments. However, in other cases, the theory-driven approach may better fit characterise the practice of hypothesisation, while the mechanism-based works better in others.

On the other hand, the theory-driven analyses (or the others) can learn from the exemplar-based approach. For example, the theory-driven analysis focuses on the activity of hypothesisation and says little on the activities of problem-defining, conceptualisation, and experimentation. Thus, the exemplar-based approach could provide a tool to make a fuller articulation of the practices framed by theories, like theory-construction and theory-confirmation. In a word, what I have aimed to do in this thesis is to propose an alternative approach to analysing and interpreting the history of genetics rather than to argue for a monistic way to understand the history of a science in general.

Exemplary Practice and Kitcher's Practice

It might seem to some that my reinterpretation of exemplar is very similar to Kitcher's notion of practice. The components of Kitcher's practice include a common language, a set of accepted statements, a set of questions, a set of patterns of reasoning, and a set of experimental procedures, while the constituents of my "exemplary practice" are a vocabulary, a set of well-defined research problems, a set of practical guides, a set of hypotheses, and a set of patterns of reasoning. Thus, some might argue that if exemplary practices are merely a reformulation of Kitcher's practices, the exemplar-based approach is also vulnerable to the objections to the theory-driven approach.

However, I argue that, despite the apparent similarity, there are substantial differences between Kitcher's "practice" and my "exemplary practice". Firstly, a set of hypotheses cannot be conflated with Kitcher's "set of statements". As I have emphasised, the hypotheses in an exemplary practice should not be simply construed as statements. Yes, in some exemplary practices, the hypotheses are originally formulated as statements (e.g. Mendel's exemplar). But the hypotheses can also appear in other forms like models and mechanism schemas. In addition, a pattern of reasoning in an exemplar is different from a pattern of reasoning in a practice. Kitcher defines a pattern of reasoning as a sequence of schematic sentences, while I refer to a pattern of reasoning as the reasoning behind the solution to the research problem in using other components of an exemplary practice.

Secondly, the significance of each component in a practice for Kitcher is different. For example, Kitcher downplays the significance of experimental procedures and methodological rules. In contrast, I contend that the vocabulary, hypotheses, experiments, practical guides, and patterns of reasoning in an exemplary practice weigh equally in the sense that they all play an important role to solve the research problems.

Thirdly, the significance of the problem is not emphasised in Kitcher's practice-based approach. In addition, although pedigree problems are important in the practice of classical genetics given that they underlie the different versions of the theory of classical genetics, Kitcher fails to articulate the pattern of the changes of pedigree problems. In other words, Kitcher overlooks the problem of problem-identification, that is, how to identify a problem in a practice.

Fourthly, Kitcher's practice-base approach, as Waters contends, is still basically theory-driven; since Kitcher contends that a practice is centred on a theory with an explanatory purpose. It is vulnerable to the objections to the theory-driven approach, while the exemplar-based one is not. Therefore, the exemplar-based approach is not a disguised practice-based approach. What is more, there is another more substantial difference.

More on Exemplar and Theory

Finally, it should be highlighted that my proposal of the exemplar-based approach should not be simply construed as a way to eliminate or overlook the role of theory in scientific practice. The traditional theory-driven approach clearly overemphasises and exaggerates the role of theory. It assumes the centrality role of some theory in a school of scientific practice. However, as I have argued in Chapter 1, theories are not the driving force of scientific practice. Nor can any theory alone be regarded as the fundamental component of the consensus among a scientific community. Nevertheless, theories are indispensable in many scientific practices. For example, the theory of pangenesis is indispensable in de Vries' 1900 works, but it is indispensable instrumentally in the sense that it is a useful tool to help define and solve the research problems. Thus, according to the exemplar-based approach, theories are important in scientific practice because they are useful to define and

solve the research problems to investigate the phenomena rather than they describe or explain the phenomena. The descriptive, explanatory, and predictive powers of a theory are the means rather than the end. In short, I argue that the significance of theory in scientific practice should not be overestimated or underestimated.

7

Conclusion

Philosophers are used to analysing the history of science with a theory-based prejudice. However, I have argued that the theory-driven analysis of the history of science is highly problematic, especially in the case of Mendelian genetics. The theory-driven approach relies on an unexamined assumption (i.e. the theory-centric view) that the history of a school of scientific practice is centred on a central theory. However, there are four main problems of taking the theory-driven approach to analysing the history of scientific practice. Firstly, it is difficult to identify and articulate a central theory for a school of scientific practice, especially in the case of Mendelian genetics. Secondly, it pays insufficient attention to how a school of scientific practice is established and develops. Thirdly, it overlooks the non-theoretical aspect of scientific practice. Fourthly, it incorrectly assumes the central role of a theory in scientific practice. In this thesis, I have proposed and defended an exemplar-based approach as a new way to analyse and understand one origin of genetics from Mendel (1865) to Bateson (1902). In short, an exemplar is defined as a set of contextually well-defined research problems and their solutions. Accordingly, a common recipe for the exemplar-based approach can be summarised in the following way.

In order to analyse the history of the practice of a scientific school, we first should

identify the initial problem as the starting point of the research¹³⁰, and then trace the way of solving the initial problem by identifying the actual problems that were investigated and the way they occur in the practice, and analysing the process of problem-defining, conceptualisation, experimentation, hypothesisation, and reasoning involved. Then, we should detail the development of the intertwined practices in history to explore the development of a school of scientific practice.

My articulation of the exemplar-based approach is based on my historical analysis of the origin of genetics. By showing Gärtner's influence on Mendel's work, I have strengthened the view that Mendel's concern (1865) was about the developmental series of pea hybrid in the progeny rather than heredity in general. Moreover, Mendel's work on *Pisum* cannot be understood as a work on heredity, whether heredity is interpreted in the 19th or 20th century sense. Furthermore, I have also challenged the traditional account of the "rediscovery" story in 1900. By examining the historical context of the "rediscoverers" carefully, I have argued that the work of "rediscoverers" should be better understood as an incorporation of Mendel's work into their own research rather than a merely rediscovery of (or reintroduction to) Mendel's work. I have strengthened the view that de Vries' initial concern (1900a, 1900c, 1900d) was to verify his hypothesis of pangenesis that the heritable trait is composed of distinct hereditary units in the cell experimentally. In particular, I have shown that in 1900 – 1903, de Vries attempted to incorporate Mendel's methodology and terminology into his theory of pangenesis, though was shown to be unsuccessful and quickly abandoned by himself shortly after. Correns' initial concern (1900) was to examine Mendel's work on *Pisum*, and ended up with a confirmation of Mendel's observations and a reformulation of Mendel's rule by incorporating Mendel's work with Weismann's terminology. Tschermak's initial concern (1900a, 1900b) was to study the influence of the foreign pollen upon the constitution of the seeds. Although his 1900 papers fail to show that he well

¹³⁰ Although I emphasised many times that one of the most important contributions of an exemplary practice is the way of defining the research problems, it is unlikely for a scientist to begin his studies without an initial problem, which was a well-defined research problem. These kind of initial problems might not be interesting at all for the subsequent development of the studies. A classical example is that the initial problem that inspired Morgan to conduct experiments on *Drosophila* was in search for an experimental approach to evolution, but he finally made a great achievement on solving the problems of *Drosophila*'s heredity. It is also likely that an initial problem is re-formulated in new terms.

understood Mendel's work, Tschermak was the first who was explicit on the point that Mendel's work would be important to the study of heredity. In addition, I have shown that he seriously attempted to develop Mendel's theory in his conceptual framework. Bateson's concern (1902) was to defend and develop a Mendelian theory of heredity against the charge by Weldon. It was the first time in the history that Mendel's work on pea hybrid was seriously introduced and incorporated into the subject of heredity.

On the basis of my historical interpretation, I have argued that Mendel's work on *Pisum* can be best characterised as an exemplary practice on the study of pea hybrid by introducing novel problem-specification, novel conceptualisation, novel hypothesisation, and novel experimentation, which were useful for the exemplary practices on the study of heredity around 1900. Similarly, de Vries', Correns', and Bateson's works can be characterised as the exemplary practices which all adopted, modified, and applied some constituents of Mendel's exemplary practice to solve their own research problems. A kind of continuity can be traced in these exemplary practices. Accordingly, the origin of genetics from Mendel (1865) to Bateson (1902) can be better characterised as a chain of successive exemplary practices than as the development of a theory, or the discovery of a mechanism. In addition, I have shown that the exemplar-based approach provides a new way to articulate a perennial puzzle in the history of genetics, namely, the problem of long neglect.

Finally, I have discussed some potential responses and challenges from the theory-driven analysis and defended the exemplar-based analysis of the origin of genetics against a potential formulation of the mechanism-based one. Nevertheless, I have to emphasise that my defence of the exemplar-based approach does not suggest that I am defending a monistic way of analysing and interpreting the history of sciences.

It should be noted that this thesis is still an incomplete attempt to explore the exemplar-based approach. Its applicability and implications are still awaiting further exploration. I believe that the exemplar-based approach is not only applicable to historical cases, but also to contemporary cases. Furthermore, taking the exemplar-based approach will also help recharacterise our philosophical views on

the nature of scientific knowledge. The habit of analysing science in terms of exemplary practices would make us realise that scientific practice is fundamentally about proposing problems and solving problems. In particular, proposing problems and solving problems are intertwined activities rather than two independent ones. Moreover, scientific confirmation and explanation can be recharacterised by taking the exemplar-based approach to be evidential practice and explanatory practice. All these will be taken into consideration of a further articulation of the exemplar-based approach in the future. In short, there is much more to do on the exemplar-based approach.

Appendix 1

Entwicklung in Mendel's Versuche über Pflanyen-Hybriden (1865)

	German Text	English Translation by Sherwood
1	die <i>Entwicklung</i> der Hybriden in ihren Nachkommen (Mendel, 1865, p. 3)	the <i>development</i> of hybrids in their progeny (Mendel, 1966a, p. 1)
2	die Bildung und <i>Entwicklung</i> der Hybriden (Mendel, 1865, p. 3)	the formation and <i>development</i> of hybrids (Mendel, 1966a, p. 2)
3	<i>Entwicklungs</i> -Geschichte (Mendel, 1865, p. 4)	<i>evolutionary</i> history (Mendel, 1966a, p. 2)
4	die Glieder der <i>Entwicklungsreihe</i> in jeder einzelnen Generation (Mendel, 1865, p. 5)	members of the <i>series</i> of offspring in each generation (Mendel, 1966a, p. 4)
5	mangelhafte <i>Entwicklung</i> des Schiffchens (Mendel, 1865, p. 10)	defective <i>development</i> of the keel (Mendel, 1966a, p. 8)
6	An einigen wenigen Pflanzen kamen in den zuerst gebildeten Hülse nur einzelne Samen zur <i>Entwicklung</i> (Mendel, 1865, p. 13)	In the pods first formed by a small number of plants only a few seeds <i>developed</i> (Mendel, 1966a, p. 11)
7	Samen, welche während ihrer <i>Entwicklung</i> von Insecten beschädigt wurden (Mendel, 1865, p. 14)	Seeds damaged during their <i>development</i> by insects (Mendel, 1966a, p. 12)
8	die <i>Entwicklungsreihe</i> für die Nachkommen der Hybriden je zweier differirender Merkmale (Mendel, 1865, p. 17)	the <i>series</i> for the progeny of plants hybrid in a pair of differing traits (Mendel, 1966a, p. 16)
9	das gefundene <i>Entwicklungs</i> -Gesetz auch dann für je zwei differirende Merkmale gelte (Mendel, 1865, p. 18)	the law of <i>development</i> thus found would also apply to a pair of differing traits (Mendel, 1966a, p. 17)
10	Die <i>Entwicklungsreihe</i> besteht demnach aus 9 Gliedern. (Mendel, 1865, p. 20)	Accordingly, the <i>series</i> consists of nine terms. (Mendel, 1966a, p. 20)
11 12	Diese <i>Entwicklungsreihe</i> ist unbestritten eine Combinationsreihe, in welcher die beiden <i>Entwicklungsreihen</i> für die Merkmale A und a, B und b gliedweise verbunden sind. (Mendel, 1865, p. 21)	Indisputably this <i>series</i> is a combination series in which the two <i>series</i> for the traits A and a, B and b are combined term by term. (Mendel, 1966a, p. 20)
13	Die <i>Entwicklungsreihe</i> umfasst 27 Glieder. (Mendel, 1865, p. 21)	The <i>series</i> comprises 27 members. (Mendel, 1966a, p. 21)
14	Die <i>Entwicklung</i> der Hybriden	The <i>development</i> of hybrids

	(Mendel, 1865, p. 22)	(Mendel, 1966a, p. 21)
15	in welcher die <i>Entwicklungsreihe</i> für die Merkmale A und a, B und b, C und c mit einander verbunden sind. (Mendel, 1865, p. 22)	in which the <i>series</i> for traits A and a, B and b, C and c are combined with each other hybrids. (Mendel, 1966a, p. 21)
16	in welchen die <i>Entwicklungsreihen</i> für je zwei differirende Merkmale verbunden sind. (Mendel, 1865, p. 22)	in which the <i>series</i> for each pair of differing traits are combined. (Mendel, 1966a, p. 22)
17	die <i>Entwicklung</i> der Hybriden bezüglich dieses Merkmales wahrscheinlich in der nämlichen Weise erfolgt (Mendel, 1865, p. 23)	<i>development</i> of the hybrids probably proceeds in the same manner with respect to this trait as it does for the remaining traits (Mendel, 1966a, p. 22-23)
18	in welcher die <i>Entwicklungsreihen</i> für je zwei differirende Merkmale vereinigt sind. (Mendel, 1865, p. 24)	in which the <i>series</i> for any one pair of differing traits are combined. (Mendel, 1966a, p. 23)
19	die <i>Entwicklung</i> der Hybriden in den einzelnen Generationen zu erklären (Mendel, 1865, p. 24-25)	to explain the <i>development</i> of hybrids in separate generations (Mendel, 1966a, p. 24)
20	Den einfachsten Fall bietet die <i>Entwicklungsreihe</i> für je zwei differirende Merkmale. (Mendel, 1865, p. 29)	The simplest case is given by the <i>series</i> for one pair of differing traits. (Mendel, 1966a, p. 29)
21	Die <i>Entwicklungsreihe</i> für Hybriden, in denen zweierlei differirende Merkmale verbunden sind, (Mendel, 1865, p. 31)	The <i>series</i> for hybrids in which two kinds of differing traits are associated (Mendel, 1966a, p. 31)
22	die <i>Entwicklungsreihe</i> der Hybriden (Mendel, 1865, p. 31)	The <i>series</i> of hybrids (Mendel, 1966a, p. 32)
23	nach welchem die <i>Entwicklung</i> der Hybriden erfolgt (Mendel, 1865, p. 32)	According to which hybrid <i>development</i> proceeds (Mendel, 1966a, p. 32)
24	das für Pisum gefundene <i>Entwicklungsgesetz</i> (Mendel, 1865, p. 32)	the <i>law of development</i> discovered for Pisum (Mendel, 1966a, p. 32)
25	die <i>Entwicklung</i> der constanten Verbindungen (Mendel, 1865, p. 32)	The <i>formation</i> of constant associations (Mendel, 1966a, p. 33)
26	die <i>Entwicklung</i> der Hybriden (Mendel, 1865, p. 34)	<i>development</i> of hybrid (Mendel, 1966a, p. 35)
27	der Combinirung der einzelnen <i>Entwicklungsreihen</i> (Mendel, 1865, p. 35)	the combination of the individual <i>series</i> (Mendel, 1966a, p. 36)
28	so entsprechen den Hybriden A ₁ a und A ₂ a die <i>Entwicklungsreihen</i> (Mendel, 1865, p. 35)	Then the <i>series</i> that correspond to hybrids A ₁ a und A ₂ a are (Mendel, 1966a, p. 36)

29	die <i>Entwicklung</i> der Culturformen (Mendel, 1865, p. 36)	the <i>development</i> of cultivated forms (Mendel, 1966a, p. 37)
30	die <i>Entwicklung</i> der Pflanze im freien Lande durch andere Gesetze geleitet wird. (Mendel, 1865, p. 36)	plant <i>development</i> in the wild and in the garden beds was governed by different laws. (Mendel, 1966a, p. 37)
31	auch hier die <i>Entwicklung</i> nach einem bestimmten Gesetze erfolgt, (Mendel, 1865, p. 38)	here, too, <i>development</i> proceeds according to a certain law (Mendel, 1966a, p. 38)
32	In Bezug auf die Gestalt der Hybriden und ihre in der Regel erfolgende <i>Entwicklung</i> (Mendel, 1865, p. 38)	With respect to the features of hybrids and their regular <i>development</i> (Mendel, 1966a, p. 39)
33	Wird angenommen, dass die <i>Entwicklung</i> der Hybriden nach dem für Pisum geltenden Gesetze erfolgte, (Mendel, 1865, p. 39)	If it is assumed that <i>development</i> of hybrid follows the law valid for Pisum (Mendel, 1966a, p. 40)
34	für 7 differirende Merkmale die <i>Entwicklungsreihe</i> (Mendel, 1865, p. 39)	the <i>series</i> for 7 differing traits (Mendel, 1966a, p. 40)
35	dann muss an den Gliedern der <i>Entwicklungsreihe</i> immer jene der beiden Stammarten mehr hervortreten, (Mendel, 1865, p. 39)	then the one of the two parental types having the larger number of dominating traits must always be the more prominent among the members of the <i>series</i> . (Mendel, 1966a, p. 40)
36	wo die <i>Entwicklung</i> eine regelmässige war (Mendel, 1865, p. 40)	where <i>development</i> was regular (Mendel, 1966a, p. 40)
37	Bei sehr ausgedehnten <i>Entwicklungsreihen</i> konnte es in der That nicht anders eintreffen. (Mendel, 1865, p. 40)	Indeed, it cannot be otherwise in very extensive <i>series</i> . (Mendel, 1966a, p. 40)
38	Für die <i>Entwicklungsgeschichte</i> der Pflanzen ist dieser Umstand von besonderer Wichtigkeit, (Mendel, 1865, p. 40)	This feature is of particular importance to the <i>evolutionary history</i> of plants, (Mendel, 1966a, p. 41)
39	Diese <i>Entwicklung</i> erfolgt nach einem constanten Gesetze, (Mendel, 1865, p. 41)	This <i>development</i> proceeds in accord with a constant law (Mendel, 1966a, p. 42)
40	dann wird die <i>Entwicklung</i> des neuen Individuums durch dasselbe Gesetz geleitet, (Mendel, 1865, p. 41)	<i>development</i> of new individual is governed by the same law (Mendel, 1966a, p. 42)
41	dessen <i>Entwicklung</i> nothwendig nach einem anderen Gesetze erfolgt, (Mendel, 1865, p. 41)	whose <i>development</i> must necessarily proceed in accord with a law different (Mendel, 1966a, p. 42)

42	der <i>Entwicklung</i> der Befruchtungszellen (Mendel, 1865, p. 42)	the <i>formation</i> of these cells (Mendel, 1966a, p. 43)
43	die <i>Entwicklung</i> der Hybriden (Mendel, 1865, p. 42)	the <i>development</i> of hybrids (Mendel, 1966a, p. 43)
44	da die Einheit im <i>Entwicklungsplane</i> des organischen Lebens ausser Frage steht. (Mendel, 1865, p. 43)	Since unity in the <i>plan of development</i> of organic life is beyond doubt. (Mendel, 1966a, p. 43)
45	Dürfte man voraussetzen, dass bei diesen Versuchen die <i>Entwicklung</i> der Formen auf eine ähnliche Weise wie bei Pisum erfolgte, (Mendel, 1865, p. 43)	If one may assume that the <i>development</i> of forms proceeded in these experiments in a manner similar to that in Pisum, (Mendel, 1966a, p. 44)

Appendix 2

Entwicklung in Gregor Mendels Briefe an Carl Nägeli

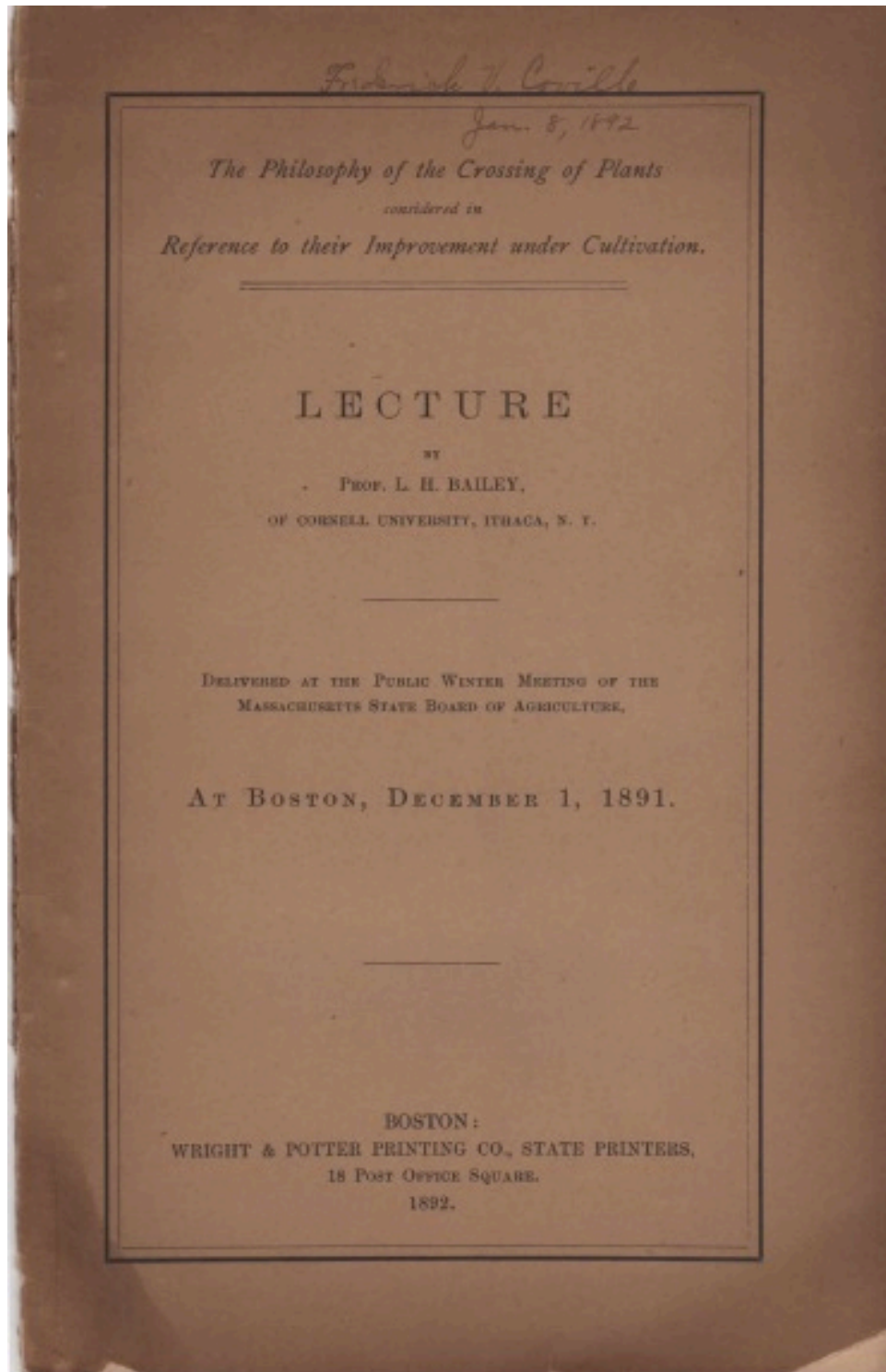
	German Text	English Translation by Piternick and Piternick
1	In den <i>Entwicklungsreihen</i> für zwei und dreierlei differierende Merkmale, ... (Correns, 1906, p. 194)	In the <i>developmental series</i> for two and three differentiating characters, ... (Piternick & Piternick, 1950, p. 1)
2	... <i>Entwicklungsgesetze</i> ... (Correns, 1906, p. 195)	... <i>laws of development</i> (Piternick & Piternick, 1950, p. 1)
3	Lassen sich für je zwei differierende Merkmale dieselben Verhältniszahlen und einfachen <i>Entwicklungsreihen</i> nachweisen, wie bei Pisum, ... (Correns, 1906, p. 195)	If for two differentiating characters, the same ratios and <i>developmental series</i> which exist in Pisum can be found, ... (Piternick & Piternick, 1950, p. 2)
4	Der <i>Entwicklungsgang</i> ... (Correns, 1906, p. 201)	The <i>course of development</i> ... (Piternick & Piternick, 1950, p. 5)
5	..., <i>Entwicklungsreihe</i> für je zwei differierende Merkmale. (Correns, 1906, p. 202)	..., <i>developmental series</i> for two differentiating characters. (Piternick & Piternick, 1950, p. 5)
6	die <i>Entwicklungsreihe</i> für aus zwei oder drei einfachen Reihen combinirt erscheint. (Correns, 1906, p. 202)	the <i>developmental series</i> is a combination of two or three simple series. (Piternick & Piternick, 1950, p. 5)
7	Wenn ich endlich die Combinirung der einfachen <i>Entwicklungsreihen</i> auf jede Anzahl von Differenzen zwischen den beiden Stammpflanzen, ... (Correns, 1906, p. 202)	If then I extend this combination of simple <i>series</i> to any number of differences between the two parental plants, ... (Piternick & Piternick, 1950, p. 5)
8	..., dass die <i>Entwicklung</i> hinsichtlich je zweier differierender Merkmale unabhängig von den übrigen Differenzen erfolgt. (Correns, 1906, p. 202)	... that the <i>development</i> of any two differentiating characteristics proceeds independently of any other differences. (Piternick & Piternick, 1950, p. 5)
9	..., weil ich in dem Resultate derselben die Erklärung für die beobachtete <i>Entwicklung</i> der Hybriden von Pisum zu finden glaube. (Correns, 1906, p. 202)	..., for I believe that their results furnish the explanation for the <i>development</i> of hybrids as observed in Pisum. (Piternick & Piternick, 1950, p. 5)
10	Für die Untersuchung der <i>Farben-Entwicklung</i> ... (Correns,	To study <i>color development</i> in flowers of hybrids, ... (Piternick & Piternick, 1950, p.

	1906, p. 210)	9)
11	... die <i>Entwicklung</i> des Pollens ... (Correns, 1906, p. 212)	... pollen <i>development</i> ... (Piternick & Piternick, 1950, p. 11)
12	In meiner Versuchsplantage haben die Pflanzen im Durchschnitte gut überwintert, auch ist die <i>Entwicklung</i> derselben ziemlich weit vorgeschritten; ... (Correns, 1906, p. 220)	On the whole the plants have wintered well in the experimental plots, and their <i>development</i> has progressed fairly well; ... (Piternick & Piternick, 1950, p. 15)
13	Ihrer weiteren <i>Entwicklung</i> sehe ich mit einiger Spannung entgegen. (Correns, 1906, p. 221)	I am awaiting their further <i>development</i> with some suspense. (Piternick & Piternick, 1950, p. 15)
14	Die Köpfschen sind auffallend gross, weit über die Mittelgrösse hinaus, was wohl nur eine Folge der sehr üppigen <i>Entwicklung</i> der Pflanze sein dürfte. (Correns, 1906, p. 223)	The heads are strikingly large, much exceeding the average, but this might be due only to the very luxuriant <i>development</i> of this plant. (Piternick & Piternick, 1950, p. 16)
15	Will man die Nachkommen jener Bastarde, die nur eine theilweise Fruchtbarkeit besitzen, in ihrer <i>Entwicklung</i> verfolgen, ... (Correns, 1906, p. 234)	If one wants to follow the <i>development</i> of those hybrids having only partial fertility, ... (Piternick & Piternick, 1950, p. 22)
16	Anfänglich schien es, als ob einzelne Pflanzen in der <i>Entwicklung</i> zurückbleiben wollten, ... (Correns, 1906, p. 239)	In the beginning it seemed as if individual plants might lag behind in <i>development</i> ; ... (Piternick & Piternick, 1950, p. 24)
17	Im letzteren Falle müsste auch die <i>Entwicklung</i> der Nachkommen eine andere sein, ... (Correns, 1906, p. 240)	In the latter case, <i>development</i> of the progeny should also be different from that in the two simple color hybrids. (Piternick & Piternick, 1950, p. 25)
18	Man erhält dann für die verschiedenen Farben Varianten Zahlen, welche für die Ableitung einer <i>Entwicklungsformel</i> unbrauchbar sind. (Correns, 1906, p. 241)	The numbers thus obtained for the frequency of the different color variants are useless for the derivation of the <i>developmental series</i> . (Piternick & Piternick, 1950, p. 25)
19	Andererseits lässt sich die Frage nicht so leicht von der Hand weisen, wenn man erwägt, dass die Anlage für die functionsfähige <i>Entwicklung</i> entweder bloß des Stempels, oder nur der Staubgefässe schon in der Organisation der Grundzellen ausgesprochen sein musste, aus welchen die Pflanzen	On the other hand the problem can not be so easily dismissed if one considers that the anlage for the functional <i>development</i> of either the pistil alone or of the anthers alone, must have been expressed in the organization of the primordial cells from which the plants developed, ... (Piternick & Piternick, 1950, p. 26)

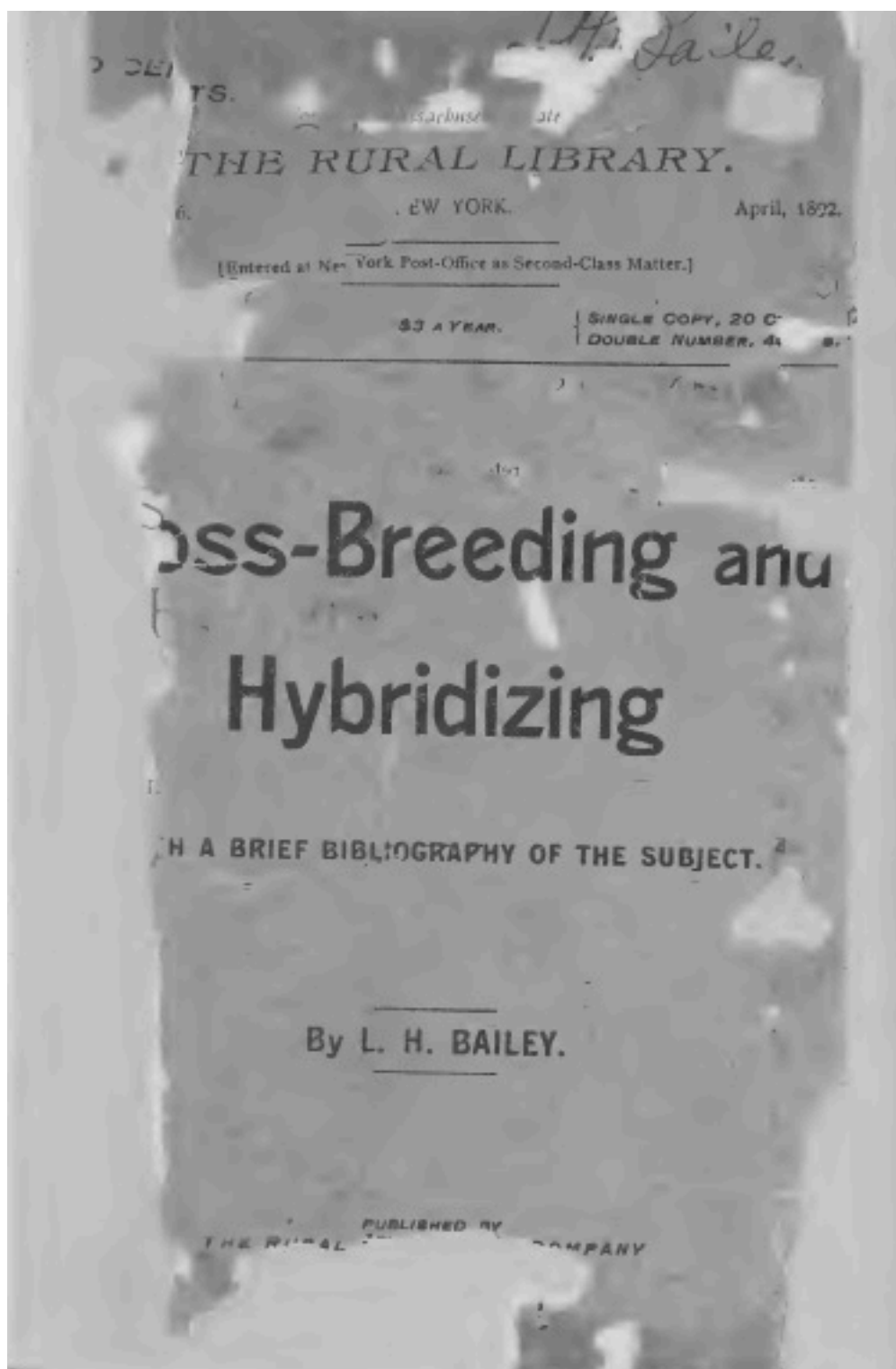
	hervorgegangen sind, ... (Correns, 1906, p. 241)	
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Appendix 3

Two Printings of L.H. Bailey's Paper *Cross-Breeding Hybridizing*



The Wright & Potter Printing (This is extracted from a copy sent by Michael Buttolph)



The Rural Library Printing (extracted from a copy downloaded from Archive.org)

Appendix 4

Evelyn Stern's Inconsistent Translation of *Eigenschaften* (de Vries, 1966)

Original Text	Translation
..., so sind sie in diesen Eigenschaften antagonistisch, ... (de Vries, 1900a, p. 84)	..., in these <i>characteristics</i> they are antagonistic, ... (de Vries, 1966, pp. 108–110)
Der Kreuzungsversuch wird dadurch auf die antagonistisch Eigenschaften beschränkt. (de Vries, 1900a, p. 84)	The crossing experiment is thereby limited to the antagonistic <i>characteristics</i> . (de Vries, 1966, p. 110)
Von den beiden antagonistischen Eigenschaften trägt der Bastard stets nur die eine, ... (de Vries, 1900a, p. 84)	Of the two antagonistic <i>characteristics</i> , the hybrid carries only one, ... (de Vries, 1966, p. 110)
Bei der Bildung des Pollens und der Eizellen trennen sich die beiden antagonistischen Eigenschaften. (de Vries, 1900a, p. 84)	In the formation of pollen and ovules the two antagonistic <i>characteristics</i> separate, ... (de Vries, 1966, p. 110)
Das Fehlen von Mittelbildungen zwischen je zwei einfachen antagonistischen Eigenschaften im Bastard ist vielleicht der beste Beweis dafür, dass solche Eigenschaften wohl abgegrenzte Einheiten. (de Vries, 1900a, p. 85)	The lack of transitional forms between any two simple antagonistic <i>characters</i> in the hybrid is perhaps the best proof that such <i>characters</i> are well delimited units. (de Vries, 1966, p. 110)
Von den beiden antagonistischen Eigenschaften (de Vries, 1900a, p. 85)	Of the two antagonistic <i>characters</i> , ... (de Vries, 1966, p. 111)
Gewöhnlich ist die systematisch höhere Eigenschaft die dominierende, oder bei bekannter Abstammung die ältere, ... (de Vries, 1900a, p. 85)	Ordinarily the <i>character</i> higher in the systematic order is the dominating one, or, in cases of known ancestry, it is the older one. (de Vries, 1966, p. 111)
IM Bastard liegen die beiden antagonistischen Eigenschaften als Anlagen neben einander. (de Vries, 1900a, p. 86)	In the hybrid the two antagonistic <i>characters</i> lie next to each other as Anlagen. (de Vries, 1966, p. 111)
Bei der Bildung der Pollenkörner und Eizellen trennen sie sich. Die einzelnen Paare antagonistischer Eigenschaften verhalten sich dabei unabhängig von einander. (de Vries, 1900a, p. 86)	In the formation of pollen grains and ovules these <i>characters</i> separate. The individual pairs of antagonistic <i>characters</i> behave independently during this process. (de Vries, 1966, p. 112)
Die Individuen d und d ² haben nur die dominierende, die Exemplare r und r ² nur die recessive Eigenschaft, während die dr offenbar Bastarde sind. (de Vries, 1900a, p. 86)	The individuals d and d ² have only the dominating <i>character</i> , those of r and r ² constitution possess only the recessive <i>character</i> , while the dr plants are obviously hybrid. (de Vries, 1966, p. 112)

Nennt man z. B. A. das eine, und B das andere Paar antagonistischer Eigenschaften, ... (de Vries, 1900a, p. 89)	If, for instance, one pair of antagonistic <i>characters</i> is called A and the other pair B, ... (de Vries, 1966, p. 116)
Wendet man ferner den Satz an, dass die Bastarde das dominirende Merkmal zur Schau tragen, so findet man für die sichtbaren Eigenschaften der Nachkommenschaft. (de Vries, 1900a, p. 89)	If one applies the rule that hybrids exhibit the dominating traits, one finds for the visible <i>characteristics</i> of the progeny. (de Vries, 1966, p. 116)
Es gelingt häufig, durch die Spaltungsveruche einfache Eigenschaften in mehrere Factoren zu zerlegen. (de Vries, 1900a, p. 89)	Success is frequently had in separating simple <i>characters</i> into a number of factors by means of segregation. (de Vries, 1966, p. 117)

Appendix 5

Entwicklung in Gärtner's Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich (1849)

	German text	English Translation	Page Number
2	<p>Durch die erste Reihe unserer Versuche, nämlich durch die Bestäubung der Narbe mit dem eigenen Pollen, suchten wir darüber Gewissheit zu erlangen: ob diese künstliche Bestäubung einen wesentlichen Unterschied von der Wirkung der natürlichen und normalen Befruchtung in Beziehung auf den <i>Entwicklungsgang</i>, und auf den Zustand der hieraus entstandenen Früchte und Samen und die Form der daraus erzeugten Pflanzen begründe? So nothwendig aber diese Versuche nach den angezeigten Rücksichten auch waren, so könnten sie bei dem stillen und geheimnissvollen Gang der Natur bei der natürlichen und künstlichen Befruchtung mit dem eigenen Pollen doch noch keine auffallende Resultate und absolute Gewissheit oder Zuverlässigkeit geben; weil aus dem Erfolge dieser künstlichen Befruchtungen die möglichen Afterbefruchtungen nicht erkennen sind: daher blieb die Fremdbestäubung und Bastardbefruchtung als der einzige sichere und zuverlässige Weg übrig, die Befruchtung der Gewächse in ein helleres Licht zu setzen, <i>der Entwicklung der Theile</i> zu verfolgen; weil der</p>	<p>Through the first series of our experiments, namely through the pollination of the stigma with their own pollen, we studied about certainty gain: whether this artificial pollination a significant difference from the effect of natural and normal fertilization in relation to the <i>course of development</i>, and on the state the resulting therefrom fruits and seeds and the shape of the plants produced from it is founded? So necessary these attempts were, however, according to the displayed considerations also, they could still be in the natural and artificial fertilization with their own pollen no striking results and absolute certainty or reliability of the silent and mysterious course of nature; because of the success of artificial insemination the possible after fertilization are not seen: therefore remained the pollination and hybridisation as the only safe and reliable way left to put the fertilization of plants in a brighter light to pursue <i>the development of the parts</i>; because the observer it hiebei longer has in his power, the beginning to determine the same, and to observe the moment of impact of the pollen, and also to put the final result in complete certainty: whether the fertilization ever succeeded, or if an error in the pollination had crept in; to give</p>	IIV - IV

	Beobachter es hiebei mehr in seiner Gewalt hat, den Beginn derselben zu bestimmen, und den Moment der Wirkung des Pollens zu beobachten, und ebenso das Endresultat in völlige Gewissheit zu setzen: ob die Befruchtung überhaupt gelungen, oder ob ein Fehler bei der Bestäubung sich eingeschlichen hatte; aus dieser Classe von Versuchen die möglichst grosse Ausdehnung zu geben.	the greatest possible expansion of this class of experiments.	
1	Wir werden daher den Grund der Seltenheit solcher Befruchtungen und des Hindernisses der Bastardbefruchtung überhaupt vorzüglich in den weiblichen Organen der Unterlage suchen müssen, was schon daraus hervorzugehen scheint, dass zuerst die Narbe den fremden Pollen schwieriger, und oft gar nicht so anzieht, dass er auf ihr haftet, obgleich die Pollenschlauche aus den Pollenkörnern durch die Narbenfeuchtigkeit zum Austreten veranlasst werden: da im Gegentheil bei der natürlichen Befruchtung, wenn auch alle Theile der weiblichen Organe <i>ihre vollständige Entwicklung</i> noch nicht erlangt haben, eine Bestäubung der Narbe mit dem eigenen Pollen sehr selten erfolglos bleibt: indem sich die Kraft des Pollens bis zum Zeitpunkt der allgemein eingetretenen Conceptionsfähigkeit der weiblichen Organe erhält: dies beweisen unsere, eigens mit friiher und später Bestäubung angestellten Versuche, wie sich	We are therefore the reason for the rarity of such fertilizations and the obstacle of hybridisation at all especially need to look into the female organs of the base, which seems to follow from the fact that first the scar the foreign pollen difficult, and often do not attract so that he on her liable, although the pollen hoses are initiated from the pollen grains by the grain moisture to escape: because on the contrary in the natural fertilization, although all parts of the female organs have not yet reached <i>their complete development</i> , pollination of the stigma with their own pollen rarely been unsuccessful: by the power of the pollen until the time of generally occurred maturity of the female organs is preserved: this prove our specially with earlier and later employed pollination experiments, as will be apparent in the episode.	9

	in der Folge ergeben wird.		
1	Bei einem grossen Theil der Bastardzeugungen der Pflanzen scheint also ein eigener günstiger Befruchtungsmoment in den weiblichen Organen, ein gewisser Hohenpunkt des Conceptionsvermögens, ein Analogon der Brunst der Thiere, nöthig zu sein, vermöge dessen nur allein bei manchen Verbindungen eine Bastardbefruchtung wirklich anschlagen kann: welcher Moment aber bei Blumen von gleicher Art und gleichem äusserlichen <i>Entwicklungsgrade</i> nicht ganz constant zu sein scheint und offenbar nicht von äusseren Verhältnissen abhängt	For a large part of the hybrid generation of the plants seems a separate cheaper fertilization moment in the female organs, a certain high point of Conceptionsvermögens, an analogue of the heat of animals to be necessary, its a hybridisation really virtue alone for some compounds may strike: what moment but not seem to be quite constant in flowers of the same type and the same external <i>developmental state</i> and apparently does not depend on outer ratios	9
1	indem die bestäubten Blumen entweder abfielen, oder doch nur unvollkommene Früchte und taube, oder nur sehr wenige gute Samen angesetzt haben: vielleicht auch deswegen, weil es wegen der Castration an <i>der Entwicklung der eigenen Wärme der Blumen fehlte</i>	by the dusty flowers either fell off, or only imperfect fruits and deaf, or very few good seeds have been used: perhaps also because it was missing because of castration on <i>the development of the own heat of flowers</i>	11
1	Wir haben die Bemerkung gemacht, dass zum Gelingen mancher Bastardbefruchtung eine wiederholte oder mehrmalige Bestäubung der Narbe mit Pollen und eine grossere Menge desselben nöthig zu sein scheint, als bei der künstlichen Befruchtung mit eigenem Pollen, z. B. bei Digitalis, Aquilegia, Potentilla, Nicotiana u. s. w., indem entweder der frisch aufgetragene Pollen immer wieder auf der Narbe verschwindet oder sich in der	We have remarked that the success of some hybridisation of the same repeated or repeated pollination of the stigma with pollen and a greater amount seems to be necessary, as in artificial insemination with own pollen, z. B. at Digitalis, Aquilegia, Potentilla, Nicotiana etc By either the freshly applied pollen disappears again and again on the scar or loses moisture in the grain; the reason thereof can be searched in various causes. 1) In the intake of grain moisture: by the pollen mixed with it; 2) the rapid penetration of the	21

	Narbenfeuchtigkeit verliert; der Grund hievon kann in verschiedenen Ursachen gesucht werden. 1) In der Ansaugung der Narbenfeuchtigkeit: indem sich der Pollen mit ihr vermengt; 2) im schnelleren Eindringen des Befruchtungsstoffs; 3) in einer ungleichformigen <i>Entwicklung der Conceptionsfähigkeit der weiblichen Organe</i> ; 4) in einem grosseren Bedarf zur Befruchtung der Eichen.	fertilization substance; 3) in a differential <i>development of maturity of the female organs</i> ; 4) of a larger need for fertilization of the oaks.	
2	Wenn eine solche durch Fremdbestäubung erzeugte Bastardfrucht in dem weiteren Verlauf ihres Wachstums, <i>etwa in der Hälfte ihrer Entwicklung</i> , anatomisch untersucht wird: so finden sich an dem Fruchthalter nur hie und da, bald an der Spitze desselben, bald in dessen Mitte, bald aber auch an der Basis unordentlich vertheilte, <i>in verschiedenen Graden der Entwicklung</i> begriffene, mit einem Embryo versehene Eichen oder Samen:	If such a hybrid fruit produced by pollination, anatomically examined in the further course of their growth, <i>about half of its development</i> : it can be found at the fruit holder only here and there, sometimes of the same at the top, sometimes in the middle, but soon messy at the base-distributed, <i>in various degrees of development</i> conceived, provided with an embryo or oak seeds:	24-25
1	besonders aber dass diese unbefruchtet gebliebene Eichen nach einem nicht sehr langen Zeitraume nach der Fremdbestäubung (s. unten von der suecessiv-gemischten Bastardbefruchtung) ihre Empfänglichkeit für die Befruchtung (selbst mit dem eigenen Pollen), sowie <i>ihr Entwicklungsvermögen</i> überhaupt verlieren	but especially that these unfertilized remaining oaks after a not very long space of time after pollination (see Fig. below of the suecessiv-mixed hybridisation) their susceptibility to fertilization (even with their own pollen), as well as <i>their potentiality of development</i> ever lose	25
1	so dass die unbefruchtet gebliebenen Eichen durch eine Nachbestäubung mit dem eigenen Pollen nicht mehr belebt und zur <i>Entwicklung</i>	so that the unfertilized remaining oaks can be no longer animated by a pollination with their own pollen, and brings to <i>development</i> , but soon assume a yellow color, shrivel	26

	erweckt werden können, sondern bald eine gelbe Farbe annehmen, einschrumpfen und verderben.	and spoil.	
1	Nun tritt aber, je nach einer vollständigeren oder unvollständigeren Schwängerung des Ovariums, ein deutlich erkennbarer Stillstand <i>der weiteren Entwicklung des Fruchtknotens</i> auf einige Tage ein und zwar bestimmter, als sich dieses nach der künstlichen Befruchtung mit dem eigenen Pollen zu erkennen gibt.	Now, however, occurs depending on a more complete or less complete impregnation of the ovary, a clearly recognizable standstill and indeed certain, when this is to recognize after artificial insemination with their own pollen <i>further development of the ovary</i> a few days.	26
1	Dieser scheinbare Stillstand in dem Wachstum der jungen Frucht <i>in der ersten Periode ihrer Entwicklung</i> ist bei den einer, längeren Zeitigungsperiode unterworfenen Gewächsen so bedeutend, dass man eher das Abfallen der, der Blume und des Griffels längst entledigten, Frucht besorgt, als am folgenden Morgen, gleichsam nach überwundenem innerem Kampfe und durchbrochenem Hinderniss, die junge Frucht ein entschiedenes Wachstum und Gedeihen zeigt.	This apparent halt in the growth of the young fruit <i>in the first period of its development</i> is so significant at the one, longer period of maturation subject growths that one rather long since the fall of, the flower of the pen and got rid of, fruit concerned, as the following morning, speak after about sore partners inner struggle and openwork obstacle, the young fruit a decided growth and prosperity shows.	27
1	zugleich scheint <i>diese Verlangsamung in der Entwicklung der Frucht</i> mit dem langsameren Gang der Befruchtung oder dem späteren Eindringen des fremden Befruchtungsstoffs in die Eichen in genauer Verbindung zustehen	at the same time seems <i>this slowdown in the development of the fruit</i> with the slower of the fertilization or the subsequent penetration of foreign material fertilization entitled in the oaks in exact conjunction	27
1	Wir werden hieraus schliessen können, dass <i>die fernere Fruchtentwicklung</i> durch ein inneres Hinderniss gestört	We are therefrom may conclude that <i>the further fruit development</i> has been disturbed by an inner obstacle: so that the fruit of their	28

	worden ist: so dass die Frucht ihr völliges Wachsthum nicht erlangen konnte, und dass diese Abortion nicht von dem gelb gewordenen Fruchtsiel, als dem ersten Zeichen der Abnahme des Wachsthums, sondern von dem Ovarium ausgegangen ist	complete growth could not attain, and that these Abortion not from the yellowed fruit stalk, as the first signs of decline of growth, but of the ovary is assumed	
1	Wenn eine solche durch Bastardzeugung entstandene Frucht <i>in der ersten Periode ihrer Entwicklung</i> im Innern untersucht wird, so findet man die befruchteten Eichen nicht in gleichem Grade der Entwicklung und der Grösse	If such a hybrid caused by procreation fruit is examined <i>in the first period of their development</i> in the interior, so no one can find the fertilized oaks in the same degree of development and the size	29
2	De Mirbel hat jedoch auch nach der natürlichen Befruchtung <i>in der ersten Periode der Entwicklung</i> in einem und demselben Ovarium die Eichen von verschiedener Grosse angetroffen. Zuweilen holen die kleineren Eichen die grosseren <i>in der weiteren Entwicklung im Wachsthum</i> wieder ein	De Mirbel, however, has encountered the oaks of various sizes even after natural fertilization <i>in the first period of development</i> in a single ovary. Sometimes bringing small oaks while bigger <i>in the further development in growth</i> again	29
1	Meistens werden nur wenige und hie und da bloß einzelne Eichen zwischen vielen anderen befruchtet; indem die unmittelbar an sie anstossenden entweder gar keine oder nur eine leichte Anregung zur <i>Entwicklung</i> erhalten haben.	In most cases, only a few here and there fertilized merely individual oaks among many others; by the abutting directly to either have received no or only a slight stimulus to <i>development</i> .	29
1	Dieser Unterschied verschwindet aber in der Folge des weiteren Wachsthums, wenn <i>das innere Hinderniss der Entwicklung</i> sich gehoben hat	But this difference disappears in the wake of further growth, when <i>the inner obstacle of development</i> has lifted itself	31
1	Die Sonnenwärme scheint daher nicht nur bios bei der Befruchtung mit fremdem Pollen (s. oben S. 10), sondern auch <i>bei der weiteren</i>	The sun's heat therefore seems to be a nothwendigere condition than in the natural fertilization not only bios at fertilization with foreign pollen (see Fig. Above, p 10), but	32

	<i>Entwicklung der Früchte und Samen</i> eine nothwendigere Bedingung zu sein, als bei der natürlichen Befruchtung.	also in the further development of fruits and seeds.	
1	Es sind von uns schon früher über fruhe und späte Bestäubung Versuche angestellt worden, um über <i>die Entwicklung und die Dauer der Conceptionsfähigkeit der weiblichen Organe der Pflanzen</i> einige nähere Kenntniss zu erhalten	There have been earlier about EARLY and late pollination employed by us attempts to get some more knowledge about <i>the development and the duration of the maturity of the female organs of plants</i>	32
1	Durch vielfältige Erfahrung belehrt, dass die bloße Verletzung oder theilweise, selbst gänzliche Hinwegnahme der Corolle der Befruchtung der Ovarien nicht den Nachtheil bringt, welchen Schelver und Henschel derselben zugeschrieben haben, haben wir drei noch enggeschlossene und <i>in gleichem Entwicklungsgrade befindliche Blumen</i> der <i>Nicotiana rustica</i> a, b und c (den 20. August 1832) in der Hälfte der Länge ihres Tubus mit aller Vorsicht quer rund herum abgeschnitten,	Through varied experience teaches that the Bloose injury or partly even utter taking away the corolla fertilization of ovaries does not bring the disadvantage which Schelver and Henschel have attributed the same, we have three more tightly closed and located <i>in the same developmental state of flowers</i> <i>Nico Liana rustica</i> a, b and c (20 August 1832) cut in half the length of its tube with caution across all around,	40
1	Von <i>Nicotiana rustica</i> haben wir (den 15. Juli 1832) neun Blumen von ganz <i>gleicher Entwicklung</i> zu gleicher Zeit castrirt.	For <i>Nicotiana rustica</i> we have (15 July 1832) nine castrated flowers are in quite the <i>same development</i> at the same time.	46
1	Es scheint also, dass die Befruchtung der <i>N. paniculata</i> mit dem Pollen der <i>N. Langsdorfii</i> erst nach 45 Minuten unter günstigen Umständen (bei + 24 R) vollbracht und Wirkung des eigenen Pollens aufgehoben wird; obgleich der grösste Theil der Eichen des Ovariums unbefruchtet geblieben war, und zu keiner <i>Entwicklung</i>	So it seems that the fertilization of <i>N. paniculata</i> with the pollen of <i>N. langsdorfii</i> only after 45 minutes under favorable circumstances (at + 24 R) accomplished and lifted action of its own pollen; although the greater part of the oaks of the ovary had remained unfertilized, and has been no <i>development</i> .	48

	gekommen ist.		
1	Diese Versuche scheinen abermals zu zeigen, dass neben den verschiedenen, dem Auge unsichtbaren <i>Entwicklungsgraden der weiblichen Organe der Gewächse</i> , die beide Agentien, das Sonnenlicht und die Wärme, (s. oben S. 10) einen grossen Einfluss auf den Gang der Befruchtung der Pflanzen haben	These experiments seem to show once again that in addition to the various sight unseen <i>the developmental state of the female organs of plants</i> , both agents, the sunlight and the heat, (see Fig. Above, p 10) have a great influence on the course of fertilization of plants	49
1	Die (im Jahr 1827) ausgesäten Samen gaben acht Pflanzen, wovon zwei bald wieder eingegangen, und sechs zur <i>völligen Entwicklung und Blüthe</i> gekommen sind; von diesen Samlingen waren vier männlich und zwei weiblich.	The (in 1827) sown seeds yielded eight plants, two of which received soon, and six came to <i>the complete development and bloom</i> ; of these seedlings were four male and two female.	49
1	Die wenigsten Blumen kamen aber zur <i>vollkommenen Entwicklung</i> , sondern die meisten derselben verdarben <i>unentwickelt</i> , besonders in der späteren Lebensperiode der Pflanze, auch hatten die wirklich <i>entwickelten Blumen</i> nur eine kurze Dauer.	But few flowers came to <i>the perfect development</i> , but most of them spoiled <i>undeveloped</i> , especially in the later period of life of the plant, also had really <i>developed flowers</i> only a short duration.	50
1	Dies ist nun ein seltener Fall einer gemischten Befruchtung; in Gewachshäusern scheinen aber solche Befruchtungen bei exotischen Gewachsen wegen unregelmässiger Blüthe und <i>Sexualorgane-Entwicklung</i> nicht selten vorzukommen, wodurch Bastardzeugungen entstehen	Now this is a rare case of a mixed fertilization; in greenhouses but seem such fertilizations often occur in exotic Grown for irregular flower and <i>sexual organs-development</i> , whereby the hybrid generation arises	51
1	weil sich bei einer unzureichenden Menge des Pollens dessen Befruchtungsstoff nicht auf einzelne Eichen zu deren Schwängerung concentrirt,	because when an insufficient amount of pollen fertilization whose substance is not concentrated on individual oaks to their Schwängerung, but by only an 'imperfect fertilization of the	56

	sondern dadurch nur eine ' unvollkommene Befruchtung des Ovariums und keine Erzeugung eines lebendigen und <i>der Entwicklung fähigen Embryos</i> bewirkt wird.	ovary and not producing a vibrant and <i>the development of the normal embryo</i> is effected.	
1	und dabei bemerkt, dass die Narben dieser Gewächse von dem Oele schwarz wurden, wie andere grüne Theile der Gewächse, wahrscheinlich weil es <i>die Gasentwicklung aus der Narbe</i> hinderte (s. oben S. 42)	and it noted that the stigmas of these growths were black from the oils, like other green parts of plants, probably because it prevented <i>the development from the stigmas</i> (see Fig. above, p 42)	60
1	Die belebende Kraft des Pollens zeigt sich vorzüglich bei der unvollkommenen Befruchtung , und ist nur ein geringerer Grad seiner schaffenden Wirkung: indem der fremde Pollen die Eichen im Ovarium nur zur Belebung und <i>Entwicklung der äusseren Umhüllungen der Samen</i> in verschiedenen Graden ihrer Ausbildung erweckt, aber nicht so viel Kraft besitzt, einen Embryo in dem Samen zu erzeugen	The animating force of the pollen shows excellently in the imperfect fertilization, and only a lesser degree of creative action is by the foreign pollen that oak brings in the ovary only for recovery and <i>development of the outer envelopes of the seeds</i> in different levels of their formation, but not so much power, holds an embryo in to generate the seed	69
1	Es ist uns noch die formbestimmende Wirkung des Pollens bei der Bastardbefruchtung zu untersuchen übrig: wir haben sie in zweifacher Beziehung zu betrachten : A) in Hinsicht der äusseren Verhältnisse der durch die Bastardbefruchtung unmittelbar erzeugten Früchte und Samen , und B) in Hinsicht der Typen, welche aus diesen Samen durch das Keimen und <i>die weitere Entwicklung der daraus hervorgegangenen Pflanzen</i> gebildet werden	We are still the shape-determining effect of the pollen on the hybridisation to investigate left: we have to consider them in double relationship: A), in respect of the external conditions of the fruit and seeds directly generated by hybridisation, and B) in terms of the types which are formed from these seeds by germination and <i>further development of the emerging plants</i> .	73
1	Vier Blumen mit dem Pollen der Vicia Faba bestäubt fielen	Four flowers pollinated with the pollen of Vicia Faba Felen after	83

	nach eilf Tagen verdorrt und ohne <i>Entwicklung des Ovariums</i> ab.	eleven days of withered and without <i>development of the ovary</i> .	
1	Die mit dem Pollen der Vicia Faba hortensis (Ackerbohne mit weisser Blüthe) und der Vicia sativa (gemeine Wicke) versuchten Bestäubungen blieben ohne Erfolg, und die Blumen fielen ohne <i>einige Entwicklung des Ovariums</i> in 16 Tagen verdorrt ab.	With the pollen of Vicia Faba hortensis (broad bean with white flower) and Vicia sativa, (common vetch) attempted pollinations were unsuccessful, and the flowers fell without <i>some development of the ovary</i> in 16 days.	85
1	dass nämlich der Einfluss des fremden Pollens nichts in den, der Mutterpflanze eigenthümlichen Formen und äusserlichen Eigenschaften der Früchte und Samen unmittelbar verändere; sondern dass nur in dem Embryo die Fähigkeit erzeugt werde, durch das Keimen und <i>die weitere Entwicklung der neuen Pflanze</i> eine Modification der betreffenden Arten und der Form ihrer Theile hervorzubringen.	namely that the influence of the foreign pollen nothing in, the mother plant peculiar shapes and external characteristics of fruits and seeds immediately alters; but that only in the embryo, the ability will produce, bring forth by the germination and <i>further development of the new plant</i> is a modification of the species concerned and the shape of their parts.	89
2	Die zweite Rücksicht der formbestimmenden Wirkung des fremden Pollens auf die Eichen der weiblichen Unterlage (s. oben S. 73) betrifft die Veränderung in der Form <i>der Entwicklung der durch die Bastardbefruchtung</i> gebildeten Keime, welche Veränderung in den Keimen zwar nicht durchs Mikroskop zu erkennen ist, die aber bei <i>der Entwicklung der Keime und ihrem Wachsthum</i> an den abweichenden Typen sich aufs Deutlichste zeigt.	The second consideration of the shape-determining effect of foreign pollen on the oaks of feminine pad (see Fig. Above, p 73) relates to the change in the form of <i>the development of the nuclei formed by the hybridisation</i> , not to see what a change in the germs through a microscope is, but with <i>the development of germs and their growth</i> on the different types, shows most clearly.	89-90
2	Lychnicucubalus albus und ruber zeigte für sich selbst nicht <i>die geringste Entwicklung des Ovariums</i> , aber mit dem Pollen	Lychnicucubalus albus and ruber did not show for themselves <i>the least development of the ovary</i> , but with the pollen of Lychnis diurna	92

	<p>der <i>Lychnis diurna</i> und <i>vesperlina</i> bestäubt entwickelten sich die äusseren Fruchthüllen, nämlich Kelch und Fruchtknoten bis auf einen gewissen Grad: das Receptaculum und die Eichen blieben aber <i>ohne Entwicklung</i>; in viel geringerem Grade erfolgte dieses durch die Bestäubung mit dem Pollen des <i>Cucubalus viscosus</i>. (S. unten Umwandlung.)</p>	<p>and vesper lina dusted the outer fruit servings, namely calyx and ovary escape disgusted to a certain degree: the receptaculum and the oaks remained but <i>without development</i>; to a much lesser degree this was done by pollination with pollen of <i>Cucubalus viscosus</i>. (See below Umwandlung.)</p>	
2	<p>Eine unvollkommene Wirkung des fremden Pollens, a. 1. eine unvollkommene Befruchtung gibt sich besonders dadurch zu erkennen, dass, wenn die Früchte auch normal zu sein scheinen, die Samen jedoch klein und mager und in <i>verschiedenen Graden der Entwicklung</i> stehen geblieben sind: dagegen aber doch die Samenrudimente, welche man von einer Blume derselben Pflanze erhält, deren Narbe nicht mit Pollen belegt worden war, an Grösse und Vollkommenheit weit übertreffen: hieraus ist zu schliessen, dass in den Eichen jener bestäubten Blumen durch den fremden Pollen eine Anregung zur <i>Entwicklung</i> bewirkt worden, ohne dass ein Embryo erzeugt worden, dass also eine unvollkommene Befruchtung erfolgt ist; hiemit stimmen auch Kölreuter's Beobachtungen überein. Befruchtung erfolgt ist; hiemit stimmen auch Kölreuter's Beobachtungen überein.</p>	<p>An imperfect effect of the foreign pollen, a first imperfect fertilization are particularly characterized to recognize that if the fruits seem to be normal, the seeds are left, however, and are small and lean in <i>different degrees of development</i>: Contrast, but but the seed rudiments which you exceed that of a flower of the same plant-keeping, whose scar was not occupied with pollen in size and perfection far: from this it can be concluded that in the oaks that pollinated flowers caused by the foreign pollen a stimulus to <i>the development</i> was without an embryo produced, so that an imperfect fertilization has taken place; hereby also agree Kölreuter's observations match.</p>	93-94
1	<p>Bei diesen zeigt sich aber</p>	<p>With these but usually shows the</p>	94

	gewöhnlich der Unterschied, dass die Ovula zwar bis auf eine gewisse Grösse wachsen, <i>dann aber in der Entwicklung stille stehen</i> , worauf die ganzen Blumen gemeiniglich abfallen	difference that while the ovules grow to a certain size, <i>but then stand still in the development</i> , whereupon the whole flowers fall commonly	
1	Bei der unvollkommenen Befruchtung aber erlangen die Eichen nicht nur in den verschiedenen Früchten derselben Art, sondern in einer und derselben Frucht <i>sehr verschiedene Grade der Entwicklung</i> , von dem einfach staubartig verlockneten Eichen bis zum vollkommenen keimungsfähigen Samen.	In the imperfect fertilization but gain the oaks not only in the different fruits of the same species, but in one and the same fruit <i>very different degrees of development</i> , from the simple dust-like rock laughed Neten oaks until the perfect sprouting of the seeds.	95
1	der Kelch erhält sich und wächst gewöhnlich noch etwas; der Fruchtknoten und seine äussere Umhüllungen bleiben aber unverändert, oder erlangen nur <i>eine geringe Entwicklung</i> , und die Eichen erfahren gar keine Anregung von einer Befruchtung: sondern verderben und vertrocknen zu staubartigenTheilen.	the cup maintains itself and grows usually still something; but the ovary and its outer wrappings remain unchanged, or acquire only <i>a small development</i> , and the oaks out any suggestion of a fertilization: but destroy and dry up to dust-like divide.	97
1	Die Bestäubung der Narbe mit Samen Lycopodii bewirkte <i>diesen Grad der Entwicklung</i> bei einigen Ovarien der Nicotiana rustica und Aquilegia vulgaris.	The pollination of the stigma with Samen Lycopodii caused <i>this degree of development</i> in some ovaries of Nicotiana rustica and Aquilegia vulgaris.	97
1	Die Blumenkrone verdirbt oder löst sich nur wenig später als bei wirklich stattfindender Befruchtung ab; Kelch und Ovarium wachsen ein wenig und entwickeln sich zu einer kleinen mageren Frucht: die Eichen aber nehmen keinen oder einen nur sehr geringen Antheil <i>an diesem Bestreben der Entwicklung</i> , sondern verderben und vertrocknen zu sehr kleinen staubartigen	The corolla corrupts or comes off a little later than in actually taking place fertilization; Calyx and ovary grow a little, and develop into a small lean fruit: the oaks take but no or only a very small part in <i>this endeavor of development</i> , but destroy and dry up to very small dust-like particles. Often the fruit of this degree falls separated long before the time of the stems from, as in the two preceding degrees.	97-98

	Partikeln. Häufig fällt die Frucht dieses Grades lange vor der Zeit vom Stiele getrennt ab, wie bei den beiden vorhergehenden Graden.		
2	Gmou de Buzareingues meint, dass zu <i>diesem Grade der Fruchtentwicklung</i> nur eine geringe Menge steriler Pollenkörner (petit nombre de grains steriles) erforderlich sei. Hier tritt namentlich bei den Hybriden der Zweifel ein: ob nicht auch der taube Pollen die Kraft besitze, die <i>Entwicklung der äusseren Umhüllungen der Frucht und der Samen</i> zu bewirken.	Gmou de Buzareingues says that at <i>this degree of fruit development</i> only a small amount of sterile pollen grains (petit nombre de grains steriles) was required. This occurs especially in the hybrids of a doubt whether even the deaf pollen possess the power to bring about <i>the development of the outer envelopes of the fruit and the seed</i> .	98
2	Bei dieser und der <i>vorhergehenden Stufe der Entwicklung der Samen</i> , wo die Testa einerseits und andererseits der Kern <i>eine weitere Entwicklung</i> erlangt, ist zu hoffen, dass unter ganz günstigen Umständen, ... doch einmal ein keimungsfähiger Embryo erzeugt werden konnte.	In this and <i>the preceding stage of development of the seed</i> , where the Testa on the one hand and on the other hand, the core attains <i>a further development</i> , it is hoped that, under very favorable circumstances, ... but once a germinable embryo could be created.	99
1	Mit mageren, seltener mit normal ausgebildeten Früchten, welche neben einer grossen Anzahl von staubartig vertrockneten Eichen und leeren Samenbälgen von <i>verschiedenen Graden der Entwicklung</i> auch einige scheinbar vollkommene Samen enthalten, die eine albuminösen Kern, aber keinen Embryo in sich festen schliessen, und daher nicht keimungsfähig sind.	With lean, rare with normal shaped fruits, which contain not only a large number of dust-like withered oaks and empty seeds with <i>different degrees of development</i> , some apparently perfect seeds, which include an albuminous core, but no embryo is fixed, and therefore not of germination have.	100
1	Die Eichen waren aber <i>in ihrer Entwicklung</i> gegen das Pericarp zurück geblieben, wurden missfarbig und	The oaks were but stayed behind <i>in their development</i> against the pericarp, were discolored and spoiled.	104

	verdorben.		
1	Eine Pflanze der Lobelia fulgenti-stiphilitica hatte aus sich selber nicht <i>die mindeste Entwicklung ihrer Fruchtknoten</i> gezeigt	A plant of Lobelia Fulgenti-stiphilitica had not shown itself <i>the least development of their ovaries</i>	104
1	dann aber standen sie auf einmal <i>in ihrer Entwicklung</i> stille, wurden gelb und schrumpften ein	but then they, suddenly silent <i>in their development</i> , were yellow and shriveled	104
1	sondern häufig nur <i>die Entwicklung der äusseren Umhüllungen der Frucht und der Samen</i> zu Stande kommt, und kein Embryo erzeugt wird.	but often only <i>the development of the outer envelopes of the fruit and the seed</i> comes to pass, and no embryo is create	104-105
1	Es bleibt daher immer noch eine unaufgeklärte Erscheinung, dass bei den Pflanzen durch die vis vegetativa (das Fruchungsvermögen) in Fällen, wo kein Atom von Pollen wirksam sein kann, ganz die gleichen Erscheinungen <i>der Entwicklung an Früchten und Samen</i> sich äussern, wie bei der unvollkommenen Bastardbefruchtung, nämlich Früchte- und Samenbildung in verschiedenen Graden der Vollkommenheit, doch mit entschiedenem Ausschluss des Embryo;	Therefore, it still remains an unexplained phenomenon that in the plants by the vis vegetativa (the Fruchungsvermögen) in cases where no atom of pollen can be effective, all the same phenomena of <i>development of fruits and seeds</i> manifest themselves, as in the imperfect hybridisation, namely fruit and seed production in various degrees of perfection, but with resolute exclusion of the embryo;	105
1	Obgleich <i>die Entwicklungsgrade der durch die Bastardbefruchtung erzeugten Früchte und Samen</i> bei den Arten der Gewächse in der Wirklichkeit nicht so genau begrenzt sind, als wir sie (oben S. 92) der genaueren Uebersicht wegen classificirt haben, sondern mehr vag und zufällig bei den gleichen Arten in verschiedenen Versuchen zu sein scheinen	Although <i>the developemental state of the fruits and seeds produced by hybridisation</i> are not limited in the species of plants in the reality as accurately as we (page 92 above) have classed the survey due to more accurate, but more vague and randomly in the same species appear to be in different experiments	106

1	Da die Früchte der wirklichen Bastarde in Beziehung <i>ihrer Entwicklung und Qualität der Pericarpn und Samen</i> mit denen aus der ursprünglichen Bastardzeugung entstandenen in manchen Stücken übereinkommen	As the fruits of real bastards incurred in relation to <i>their development and quality of pericarps and seeds</i> with those from the original Bastard procreation agree in many respects	106
1	Auch Prof. Hornschuch hält die hybride Abkunft dieser Farne für unwahrscheinlich, und vielmehr für <i>verschiedene Entwicklungsstufen einer Formenreihe</i> und durch zufällige aussere Einflüsse entstandene Zwischenformen.	Also Prof. Horn Schuch keeps the hybrid origin of these ferns for unlikely and rather for <i>different stages of development of a series of forms</i> and caused by accidental outer influences intermediate forms.	119
1	Wenn wir voraussetzen dürfen, dass bei diesen Beobachtungen auf die grossen Veränderungen der Blätter der Farnkrautsämlinge im Fortschritt <i>ihrer Entwicklung</i> , wie sie auch bei anderen Gattungen stattfinden, Rücksicht genommen worden ist	Has been, if we may assume that these observations to the large changes in the leaves of fern seedlings progress in <i>their development</i> , as they also occur in other species, taken into consideration	119
1	Prof. H. F. Autenrieth erwähnt einer Verbindung zwischen Carica Papaja und Cucumis Melo, welche dem botanischen Gärtner H. Ortmann in Tübingen gelungen sei, deren Sämlinge aber noch <i>vor ihrer vollkommenen Entwicklung</i> zu Grunde gegangen seien.	Prof. HF Autenrieth mentioned a connection between Carica papaya and Cucumis Melo which the botanical Gärtner H. Ortmann was succeeded in Tübingen, whose seedlings were but perished <i>before their perfect development</i> .	133
1	Die Frage, worin sich die Art von der Varietät unterscheidet, ist daher, wie E. Fries bemerkt, eine rein biologische; indera ein sicherer Grund der Artbestimmung nicht bios in der Abstraktion gefunden werden kann, weder in den Merkmalen noch in den Uebergangsformen; sondern man muss ihn in der Reflexion suchen, d. h. in der	The question of what the nature of the Varietät distinguish, therefore, as E. Fries noted, a purely biological; indera a secure base the identification of species can not be found in the bios abstraction, neither in the features still in the transitional forms; but you must seek him in the reflection, ie. within the individual story of each species, <i>their whole development</i> , and not	151

	individuellen Geschichte einer jeden Art, <i>deren ganzen Entwicklung</i> , und nicht in einem gewissen Moment.	at a certain moment	
1	Der Wechsel des pflanzlichen Organismus, seine Veränderungen und Verwandlungen erfolgen gewiss nach bestimmten Gesetzen, und der Lauf der Veränderungen der Pflanzenspecies wird bei den vollkommeneren Gewächsen durch den ewigen Wechsel des Absterbens und die Wiederenstehung durch die geschlechtliche Zeugung, durch <i>die Entwicklung aus dem Keim</i> , das Wachstum und die Metamorphose der Theile vollbracht und erschöpft, und die Art (Species) durch diesen ewigen Kreislauf erneuert und in ihrem Wesen erhalten, ohne dass ihre Natur und ihr Grundtypus eine wesentliche Veränderung erlitte.	The change of the plant organism, its changes and transformations take place certainly according to certain laws, and is the way of the changes in the plant species in the more perfect plants through the eternal exchange of dying and the re-emergence of the sexual generation, through <i>the development of the germ</i> , the growth and metamorphosis of the parts done and exhausted, and the type (species) of this eternal cycle renewed and receive its essence without their nature and basic type would suffer a substantial alteration.	161
1	der Pollen kann aber für seine Art vollkommen potent, aber doch unvernünftig sein, das Ovarium einer anderen, obgleich sehr nahe verwandten, Art auch nur zu <i>einiger Entwicklung</i> anzuregen, geschweige wirklich zu befruchten (s. unvollkommene Befruchtung);	the pollen can also be for his type perfectly potent, but incapable, also stimulate the ovary to another, although very closely related, species only <i>some development</i> , let alone actually fertilize (s imperfect fertilization.);	183
1	Die verschiedenen Grade der sexuellen Affinität treten aber <i>in dem weiteren Verlauf der Entwicklung der Ovarien</i> , ganz besonders aber in der grösseren oder geringeren Vollkommenheit der Früchte und Samen und vorzüglich in der geringeren oder grösseren Anzahl von guten	The various degrees of sexual affinity occur but produce <i>in the further course of development of the ovaries</i> , but especially in giving the greater or less perfection of the fruit and seeds and vorzüglich in the smaller or larger size number of good keimungsfähigen seeds.	189

	keimungsfähigen Samen hervor.		
1	Die Früchte wachsen und vergrössern sich beinahe bis zur Vollkommenheit, und erreichen fast ihre vollständige Grösse: ohne dass jedoch die Samen <i>ihre gehörige Entwicklung</i> erhalten.	The fruits grow and enlarge almost to the full Komen awareness, and reach almost their full plete Size: without, however, the seeds get <i>their proper development</i> .	190
1	Die Fruchtsiele bekommen dann am Verbindungsgelenk einen gelben Ring und fallen hierauf immer unreif ab, zu einer Zeit, wo die Samen <i>ihre weitere Entwicklung</i> und Ausbildung erhalten sollten: obgleich die äusseren Fruchthüllen das, in dieser Periode angemessene Wachsthum beinahe erreicht hatten.	The fruit stalks then get a yellow ring at the connecting joint and fall thereon from always immature, at a time where the seeds should receive <i>their further development</i> and training: although the outer fruit servings had the almost achieved reasonable growth in this period.	190
1	doch ist auch hier im freien Stand der Natur der Unterschied selten so gross, dass man <i>in den Früchten von normaler Grösse und Entwicklung</i> nicht einen Anhaltspunkt finden, und durch Zählung der Samen von mehreren vollkommenen Früchten ein Mittel erheben könnte	but the difference is also seldom so large that you can not find a clue <i>in the fruits of normal size and development</i> in the free state of nature, and could raise a means by counting the seeds of several perfect fruit	207
1	Beweis gegen die Schleiden'sche Entstehungstheorie des Embrzo aus dem Ende des Pollenschlauchs; denn wie könnte aus zwei ganz verschiedenen Arten von Pollen der vollkommen gleiche Embryo mity seinem ganz <i>gleichen Entwicklungstypus</i> hervorgehen?	Evidence against the theory of the origin of the Schleiden'sche Embrzo from the end of the pollen tube; for how could emerge from two very different types of pollen from the same embryo completely mity his very <i>same type of development</i> ?	230
1	Eine jede Frucht mit den daraus erhaltenen Samen wurde abgesondert gehalten und für sich ausgesät, und ein	Each fruit with the seeds obtained therefrom was kept isolated and seeded for themselves, and special attention given to ensuring that at	233

	<p>besonderes Augenmerk darauf gerichtet, dass bei der Aussaat kein Samenkorn, und nach dem Keimen kein einziges Keimpflänzchen verloren, sondern alle in einer Frucht erhaltenen Samen zur <i>völligen Entwicklung ihrer Pflanzen</i> gelangen möchten, damit nicht in einem oder dem anderen Samen oder Sämlinge eine abweichende Form zu Grunde gehen möchte, welche für das Hauptresultat der Normalität oder Unstätigkeit der Bastardtypen von Wichtigkeit oder Einfluss hätte sein können.</p>	<p>sowing no seed, and after germination lost a single seed plants, but all seeds obtained in a fruit to <i>complete development of their plant</i>, so not in one or the other seeds or seedlings would like to go a different shape to reason, which would for the main result of the normality or Unstätigkeit the bastard types of importance or influence can be.</p>	
1	<p>Hauptsächlich ist über die Beobachtung Kölreuteräs zu bemerken, dass, da <i>die vollendete Entwicklung und Zeitigung der Früchte</i> dieser Tinkturen nicht abgewartet worden, und der Zustand der Samen unentschieden geblieben ist, diese Beobachtung eines vollständigen Beweises entbehrt</p>	<p>Mainly it is noted on the observation Kölreuteräs that since <i>the completed development and maturation of the fruits</i> of these tinctures have not waited, and the condition of the seeds remained undecided, this observation lacks a complete proof</p>	246
1	<p>Es kann hier auch noch die Frage entstehen: ob nicht <i>ein verschiedener Entwicklungszustand der Narbe</i> bei der Befruchtung einen Einfluss auf die Typen der Bastarde habe, und zu diesen Tinkturen Veranlassung geben könnte?</p>	<p>It can also still arise the question whether <i>a different developmental state of the stigma</i> at fertilization have an impact on the types of hybrids have, and could give rise to these tinctures authority?</p>	248
	<p>Bei der einfachen Bastard Zeugung sind nämlich zwei Faktoren, der mütterliche und der väterliche, von zwei verschiedenen Pflanzenarten thätig, wovon jede ihre eigene Natur und Bildungskraft und <i>ihre eigenthümliche</i></p>	<p>In simple hybrid genesis two factors, the maternal and paternal of, from two different plant species are in fact active, each of which its own nature and formation force and <i>their peculiar form and develop the characters possessing</i></p>	254

	<i>Entwicklung und Ausbildung der Charaktere besitzt</i>		
1	denn im ersten Fall hat die Menge des zur Befruchtung eines Ovariums angewandten Pollens nur auf die Menge und Qualität des zur <i>Entwicklung</i> kommenden Samens Einfluss	because in the first case, the amount of procedure used to fertilize an ovary pollen only on the quantity and quality of seeds coming to <i>development</i> influence	274
2	Da es uns noch an Mitteln fehlt, die Entstehung und <i>Entwicklung der verschiedenen Pflanzenformen</i> von der einfachen Zelle an bis zur vollendeten <i>Entwicklung des vollkommenen Gewächses</i> in ihren verschiedenen Phasen zu erklären und im Organismus zu verfolgen oder zu construiren: so sind wir auch noch nicht im Stande, die Bande zu bestimmen, womit der Metaschematismus der hybriden Bildung mit der vegetabilischen Metamorphose überhaupt zusammenhängt.	Because there we still lack of means, to declare in its various phases and to follow in the organism or to construct the origin and <i>development of the various forms of plants</i> from simple cell to at <i>completed development of the perfect crop</i> : we are not even able to determine the band, bringing the Metaschematismus of hybrid formation with the vegetable metamorphosis at all related.	293
1	L.C. Marquart hält zwar Weiss für eine Uebergangsstufe zwischen grün und blau, und es ist nicht zu läugnen, dass wie schon Meyen bemerkt hat, in den meisten Fällen entweder <i>in dem Anfang der Entwicklung der weissen Blumen</i> oder bald nach ihrem vollendeten Vigor sich irgend ein anderer Farbenton zu erkennen gibt.	L.C. Although Marquart holding white for a transition stage between green and blue, and it can not be denied, that has as already noted Meyen, in most cases, either <i>in the early development of white flowers</i> or soon after the ages of Vigor is any other hue are recognized.	306
1	Die weissen Blumen sind vor <i>ihrer Entwicklung</i> in den Knospen entweder grün oder gelblich.	The white flowers are in front of <i>their development</i> in the bud either green or yellow.	306
1	so dass an einer und derselben Pflanze, je nach dem Alter und <i>dem Entwicklungsgrade der Blumen</i> und der Einwirkung des Lichts und der Sonne sehr verschieden stark gefärbte Blumen angetroffen werden.	so that at one and the same plant, depending on the age and <i>the developmental stage of the flowers</i> and the action of light and the sun very different highly colored flowers are found.	312

1	Demnach gingen bei der Zea Mays nana aus Einer Zeugung durch die ursprüngliche Bastardbefruchtung äusserlich ganz gleiche, von denen der Stammutter nicht verschiedene Samen hervor, welche erst <i>in der weiteren Entwicklung der Keimpflanzen</i> verschieden gefärbte Samen erzeugten	Thus went in Zea Mays nana from one generation by the original hybridisation externally very similar, of which the ancestress not different seeds produced, which produced only <i>in the further development of the seedlings</i> differently colored seeds	323
1	sondern in dem Embryo nur die Fähigkeit erzeugt, durch das Keimen und die <i>weitere Entwicklung der neuen Pflanze</i> ein aus beiden concurrirenden Faktoren vermischtes Produkt hervorzubringen.	but in the embryo produces only the ability to produce a blended product of both factors concurrirenden by the germination and <i>further development of the new plant.</i>	327
1	Nachdem wir die Bastardzeugung von ihrem Anfang an bis zur <i>völligen Entwicklung der aus den erzeugten Samen hervorgegangenen Pflanzen nach ihren verschiedenen Phasen</i> verfolgt haben	After we have followed the bastard generation of its beginning until <i>the complete development of the plants produced from the seeds according to their different phases</i>	329
1	Da die männlichen Organe der Pflanzen in den Blumen die früheren <i>in der Entwicklung und Reife</i> sind:	Since the male organs of plants the earlier <i>in the development and maturity</i> are in the flowers:	329
1	Unzählige Blumen dieses äusserst floriden Bastards sind auch nach der künstlichen Bestäubung, nachdem die Corolle vorher verdorben und eingeschrumpft sich abgestossen hatte, ohne <i>alle Entwicklung des Ovariums</i> am dritten vierten Tage abgefallen.	Countless flowers this extremely florid hybrids are also after the künstlichen pollination after the corolla spoiled before and had shrunk repelled by it, dropped without <i>any development of the ovary</i> on the third fourth day.	338
1	Aus der beschränkten und häufig gänzlich fehlenden Potenz der Stauborgane der Bastarde sind wir geneigt, auf einen Mangel <i>der Wärmeentwicklung in deren Blumen</i> zu schliessen; da zur Potenzierung des Pollens nicht	From the limited and often complete lack of potency of the dust organs of the bastards we are inclined to infer a lack of <i>heat development in their flowers</i> ; because not only external, but also internal heat appears to be required for potentiation of pollen.	341

	nur äussere, sondern auch innere Wärme erforderlich zu sein scheint.		
1	oder sind solche unvollkommene Früchte dem allgemeinen Fruchtvormögen zuzuschreiben, welches durch die Bestäubung der Narbe auch mit indifferenten Stoffen zu einer <i>theilweisen Entwicklung der Ovarien</i> unter besonderen Umständen zuweilen angeregt zu werden scheint, wie wir nicht selten bei Dianthus und Digitalis - Bastarden sehen	or are those imperfect fruits attributed to the general Fruchtvormögen, which seems to be inspired by the pollination of the scar with inert materials to <i>this partial development of the ovaries</i> under besonderen circumstances sometimes, as we often at dianthus and digitalis - see hybrids	341
1	weil die sterilen Fruchtknoten dieselben Erscheinungen und Veränderungen im Laufe <i>ihrer Entwicklung</i> vor dem Zeitpunkt der Befruchtung darbieten, welche die reinen Arten in der gleichen Periode ihres Wachstums zeigen, worin Kolreuter und Prof Wiegmann mit uns übereinstimmen.	because the sterile ovary same phenomena and changes in the course of <i>their development</i> before the date of fertilization present, showing the pure species in the same period of their growth, which Kolreuter and Prof Wiegmann agree with us.	342
1	In einer späteren Periode, wenn <i>die Entwicklung der Blumen</i> der, mit schwachem oder gänzlich mangelndem Conceptionsvermögen begabten weiblichen Organe weiter vorgeschritten ist: so haben wir jedoch zweierlei Erscheinungen an denselben beobachtet, welche mit ziemlicher Wahrscheinlichkeit auf ihre sehr beschränkte oder gänzlich mangelnde Fruchtbarkeit schliessen lassen.	At a later period, when <i>the development of flowers</i> , gifted with weak or entirely lack Conceptionsvermögen female organs is more advanced: so, however, we have two phenomena observed in the same, which can include quite possibly on their very limited or completely lack of fertility.	342
1	Die Bestäubung der Narben dieses Bastards mit dem Pollen der <i>Lzchnis diurna</i> äusserte eine entschiedenere Wirkung auf die Ovarien dieses Bastards: es entstanden zwar auch nur	The pollination of the genesis of this hybrid with the pollen of the <i>Lzchnis diurna</i> expressed a more decisive effect on the ovaries of this hybrids: Although it just goes back to small imperfect fruit, in	346

	<p>kleine unvollkommene Früchte, in welchen sich weder das Receptaculum, noch die Ovula im geringsten entwickelthatten: aber der Kelch und die äussere Umhüllung der Frucht gelangte zu mehr Ausbildung, und es bildete sich eine härtere Schale: da im Gegentheil diejenigen Blumen, welche sich selbst überlassen blieben und nicht bestäubt worden waren, nicht das geringste Zeichen <i>einer weiteren Entwicklung</i> gezeigt haben.</p>	<p>which neither the receptaculum, nor the ovules in the least developed had: but the calice and the outer envelope of the fruit reached more training, and it formed a harder shell: since on the contrary those flowers which themselves were left and had not been pollinated, have not shown the slightest sign of <i>a further development</i>.</p>	
1	<p>Der Kelch des Lychnicucubalus albus bläht sich nach dem Abbliihen kugelförmig auf, es setzen aber keine Friichte an, und <i>die Ovarien bleiben ohne alle Entwicklung</i>, und vertrocknen zu kleinen knopfförmigen Körperchen.</p>	<p>The cup of Lychnicucubalus albus inflates after the Abbliihen spherical, but it set no Friichte, and <i>the ovaries remain without any development</i>, and to dry up small button-shaped bodies.</p>	346
1	<p>Die Verbindung der Lychnis diurna mit der Silene noctiflora, welche nur für eine Varietät von der L. diurna angesehen werden könnte hatte in den Befruchtungsorganen des erzeugten Bastards nicht die gleiche Wirkung, wie bei den vorigen aus diclinischen und hermaphroditischen Gewächsen gebildeten Hybriden; indem die Anzahl der Griffel von der Mutter in alien Blumen unverändert geblieben, und die Conceptionsfähigkeit nicht geschwächt war: die Rudimente der mannlichen Organe aber mehr zur <i>theilweisen Entwicklung</i> gekornmen waren, wodurch die Neigung zum Cryptohermaphroditismus vermehrt worden ist.</p>	<p>The compound of Lychnis diurna with the Silene noctiflora, which could be considered only for a variety of the L. diurna had not diclinischen in the organs of fertilization Bastards produced the same effect as in the previous and hermaphroditic plants hybrids formed; by the number of pens from the mother in alien flowers remained unchanged, and the maturity was not weakened: the rudiments of male organs, however, were more gekornmen for <i>this partial development</i>, thereby reducing the tendency has been increased to Cryptohermaphroditismus.</p>	347

1	In Beziehung auf den Zustand der männlichen Organe haben wir auch die kurzen pyramidalischen, drüsenartigen Rudimente des Staubfädenkranzes der <i>L. vespertina</i> niemals zu <i>einer weiteren Entwicklung</i> gelangen sehen; aber bei der <i>L. diurna</i> die eine oder die andere der rudimentären Antheren in einzelnen weiblichen Blumen in diesem oder jenem Exemplar zuweilen theilweise so weit entwickelt gefunden, dass sie etwas potenten Pollen erzeugten, welcher zur Befruchtung eines oder einiger Eichen seines Ovariums zureichend war, wodurch dann ein einziger oder auch einige vollkommene keimungsfähige Samen hervorgebracht wurden.	In relation to the condition of the male organs, we also see the short pyramidal, glandular rudiments of stamens ring of <i>L. vespertina</i> never reach <i>a further development</i> ; but in <i>L. diurna</i> one or the other of the rudimentary anthers in single female flowers in this or that instance sometimes partially developed so far found that they produced something potent pollen which one or some of its oaks ovary was insufficient for fertilization, which then a single or even a few perfect keimungsfähige seeds were produced.	349
1	Als allgemeines Resultat hat sich aus unseren Versuchen ergeben, dass die Befruchtungsthätigkeiten, die männliche sowohl, als die weibliche, in alien Bastarden (die Varietätenbastarde etwa allein ausgenommen) geschwächt und in sehr vielen gänzlich zerstört sind: so dass man versucht sein könnte, zu schliessen, dass die beiden Geschlechter im pflanzlichen Hermaphroditisms, in einem nothwendigen <i>Entwicklungsnexus</i> mit einander stehen, und nur unter gewissen Bedingungen von einander getrennt angetroffen würden	As a general result has emerged from our experiments that the Befruchtungsthätigkeiten that manly either, as the female, in alien hybrids (the Varietätenbastarde about alone excepted) are weakened and completely destroyed in very many: so that one might be tempted to conclude that the two sexes were found separately in the plant Hermaphroditisms, in a necessary <i>developmental connections</i> are with each other, and only under certain conditions from each	353
4	wenn wir endlich noch einzelne Erscheinungen <i>der Entwicklung der Geschlechtsorgane</i> bei den	when we finally pull even individual phenomena of <i>the development of the sex organs</i> in the plant into consideration, for	354

	<p>Pflanzen in Betrachtung ziehen, z. B. dass mit der Verkümmern (Contabescenz) der Staubgefäße in manchen Blumen die Frühzeitigkeit des Conceptionsvermögens der weiblichen Organe gewöhnlich verbunden ist (was übrigens doch nicht immer stattfindet; indem z. B. bei Geum, Primula u. a. die frühzeitigen Griffel von den normalen Staubgefäßen im Wachsthum und <i>in der vollkommenen Entwicklung</i> wieder eingeholt worden sind,) und auf der anderen Seite mit <i>einer frühzeitigen Entwicklung der männlichen Organe und ihrer Kraft in den Blumen</i> die später eintretende Zeugungsfähigkeit der weiblichen Organe normal verbunden ist: so könnte man den obigen Schluss noch mehr begründet finden und aus allem Diesem noch weiter folgern, dass die beiden Geschlechtsorgane und ihre Thätigkeiten, sowie <i>ihre Entwicklung in den hermaphroditischen Blumen</i> in einem ursächlichen Zusammenhang mit einander stehen</p>	<p>example, with stunting (Contabescenz) of stamens is that the earliness of Conceptionsvermögens the female organs usually connected in some flowers (which by the way but does not always occur,. using eg when Geum, Primula have been obtained including the early style of the normal stamens in growth and <i>in perfect development</i> again), and on the other side with <i>an early development of male organs and their power in the flower</i> the subsequent relevant fertility of the female organs is normally connected: one might find even more reasons to the above conclusion from all this and conclude further that the two sexual organs and their Thätigkeiten, as well as <i>their development in the hermaphroditic flowers</i> are in a causal relationship with each other.</p>	
1	<p>Dass aber die männlichen Organe vor den weiblichen durch den Hybridismus krankhaft afficirt werden, scheint seinen natürlichen Grund <i>in der normalen frühzeitigen Entwicklung der männlichen Organe</i> von den weiblichen zuhaben: und dass sie mehr leiden und später wieder zu ihrer Integrität zurückkehren, beweist nur, dass die beiden</p>	<p>But that the male organs are morbidly affected in front of the female by the Hybridismus, seems its natural base <i>in the normal early development of the male organs of the female</i> to have: and that they suffer more and later return to their integrity again, only proves that the two organs of generation on Material, as are their powers in any way related context both in relationship.</p>	355

	Zeugungsorgane sowohl in Beziehung aufs Materielle, als auf ihre Kräfte in keinem so nahen Zusammenhang stehen.		
1	Auf der anderen Seite findet man aber auch manche normale Dichogamen, wie <i>Lychnis diurna</i> , <i>Cannabis sativa</i> , <i>Mercurialis annua</i> u. a. durch <i>Entwicklung und Ausbildung eines oder mehrerer Rudimente der männlichen Organe</i> in den weiblichen Blumen in unvollständig hermaphroditische sich verwandeln.	On the other hand, there are also some normal Dichogamen as <i>Lychnis diurna</i> , <i>Cannabis sativa</i> , <i>Mercurialis annua</i> including through <i>development and training of one or more rudiments of male organs</i> in the female flowers in incomplete hermaphroditic turn.	361
1	Zuweilen erfolgt aber auch <i>die Entwicklung solcher Staubgefäße in dieser oder jener Blume</i> auf eine vollständigere Weise: wie wir dies bei <i>Spinacia</i> , <i>Cannabis</i> und <i>Mercurialis</i> angetroffen haben, wo sich manche Blume zur vollständigen hermaphroditischen entwickelt und dadurch mehrere benachbarte weibliche Ovarien befruchtet hatte.	But sometimes also takes <i>the development of such Stamens in this or that flower</i> in a more complete way: as we have encountered in <i>Spinacia</i> , <i>cannabis</i> and <i>Mercurialis</i> , where some flower full news hermaphroditic developed and characterized several adjacent female ovaries had fertilized.	362
1	Das weibliche Rudiment in der männlichen Blume scheint aber bei den meisten dieser Gewächse, wenigstens in den genannten und von uns genauer untersuchten Pflanzen zu unvollkommen und die morphologische Kraft in dem männlichen Individuum überhaupt zu schwach zu sein, als dass es <i>einer weiteren Entwicklung</i> zu einem conceptionsfähigen Pistill fähig wäre	But the female rudiment in male flower seems the morphological force to be imperfect and in the male individual in general too weak for most of these plants, at least in those and we precisely investigated plants, as <i>it further development</i> to a conceptionsfähigen would be able pestle	362
1	Dass aber die Wiederherstellung der Staubgefäße in ihre normale	But that the restoration of stamens in their normal Integrilät both in form, but particularly is slower and	363

	<p>Integrilität sowohl nach Form, besonders aber nach der ursprünglichen Kraft bei der Urn- und Rückbildung langsamer und einige Generationen später erfolgt; davon finden wir in der Natur der Gewächse und der Metamorphose der Blumen noch keine genügende Erklärung. Steht diese Thatsache nicht im Widerspruch mit der Behauptung: dass die weiblichen Organe der Gewächse <i>ein höherer Grad der pflanzlichen Bildung und Entwicklung</i> seien, als die männlichen, wie Schelver und Engelmann behaupten?</p>	<p>some generations later after the original force in the URN and regression; which we find in the nature of plants and the metamorphosis of flowers still no satisfactory explanation. If this fact is not in contradiction with the assertion that the female organs of plants, <i>a higher degree of plant formation and development</i> are the male, as Schelver and Engelmann say?</p>	
1	<p>Bei der Rückbildung und der Umwandlung der Bastarde ist daher die Castration der Blumen nicht nothwendig: denn der Pollen der Stammeltern macht den eigenen des Bastards völlig unwirksam: wie der stammelterliche Pollen selbst bei manchen absolut sterilen Bastarden dadurch noch einige Einwirkung auf die damit bestäubte Blume zu äusseren scheint, dass dieselbe sich mehrere Tage länger frisch am Stocke erhält, ohne dass jedoch der Fruchtknoten und die Eichen ein Zeichen <i>einer Entwicklung zu erkennen</i> geben</p>	<p>In the regression and the Umwandlung the bastards therefore castration of flowers is not necessary: because the pollen of the first parents make their own the Bastards completely ineffective: as the originating parental pollen itself in some absolutely sterile hybrids by some action on the so-pollinated flower to outer seems that the same several days fresher longer gets on the stick, but without the ovary and nevertheless <i>reveal a sign of development</i> of oaks</p>	364
1	<p>Die Zeugungskraft der reinen Arten ist zwar in der ersten Periode <i>ihrer Blütenentwicklung</i> gewöhnlich von mehr Fruchtbarkeit begleitet als in der späteren Periode</p>	<p>The generative power of pure species is indeed in the first period of <i>their flower-development</i> usually accompanied by more fertility than in the later period</p>	

1	<p>Wohl haben wir von einigen reinen Arten der Diclinen Beispiele, dass sich die Geschlechtsverhältnisse in den Individuen mit den Jahren verändert haben, wie wir von der <i>Myristica</i> und von <i>Corylus</i>, erfahren haben, bei welcher letzteren die weiblichen Blumen ein Jahr später als die männlichen zur <i>Entwicklung</i> kamen.</p>	<p>Well we have of some pure types of Diclinen examples that the sex ratios have changed in individuals over the years, as we have learned from the <i>Myristica</i> and <i>Corylus</i>, in what the female flowers latter one year later than the male to the <i>development</i> came.</p>	368
1	<p>Wie Klima, Witterung, Boden u. s. w. auf die Pflanzen überhaupt und ihre Fruchtbarkeit insbesondere einen nicht zu bestreitenden Einfluss haben, (s. nnten Fruchtbarkeit der Bastarde), so mag dies noch in höherem Grade bei den Bastarden der Fall sein, weil bei ihnen ein gestörtes Verhältniss der zeugenden Kräfte an sich stattfindet: dieser Einfluss scheint aber nur auf <i>die Entwicklung der vorhandenen Anlage</i>, nicht auf die specielle Bestimmung des Geschlechts zu gehen, welcher Meinung auch G. R. Treviranus ist</p>	<p>How climate, weather, soil u. S. W. at all on the plants and their fertility in particular have an undeniable influence (see Fig. Nnten fertility of hybrids), so this may still higher degree when the bastards be the case, because with them a disturbed relation of the creative forces takes place in itself: this influence appears only on <i>the development of the existing system</i>, not to go to the especial determination of sex, which is also the opinion GR Treviranus</p>	370
1	<p>Die ausserordentliche Produktivität in Blumen, welche von alien Beobachtern, die sich der Bestarderzeugung gewidmet haben, bestätigt wird , mag die unmittelbare Folge der Schwachung der Zeugungskrafte der Bastarde sein; so dass dieselbe in geradem Verhältniss mit der Sterilität derselben zu stehen scheint, und wovon wir keine Ausnahme beobachtet haben; weil selbst die fruchtbarsten Hybriden ungleich mehr</p>	<p>The extraordinary productivity in flowers, which of alien observers who have devoted themselves to the Bestarderzeugung is confirmed, may be the direct consequence of the weakening of the forces generating the bastards; so that the same in direct ratio with the same sterility seems to be, and what we have observed no exception; because even the most fertile hybrids display far more infertile than fertile flowers, and even these besitzten only one-Limited fertility (see Fig.</p>	372

	unfruchtbare als fruchtbare Blumen tragen, und selbst diese nur eine beschränkte Fruchtbarkeit besitzen (s. <i>unten Blumenentwicklung</i>).	<i>flower-development below</i>).	
1	Bei sehr vielen Gewachsen kommt aber die ursprüngliche Frucht- und Samenanlage normal niemals oder doch äusserst selten zu ihrer vollen Ausbildung: wobei man annehmen kann, dass dies nicht von dem Mangel des befruchtenden männlichen Stoffes, sondern von einer, in der ganzen Pflanze liegenden Disposition, einem besonderen Bildungstrieb herrühre, welcher <i>die Entwicklung der Anlage</i> hindert	For very many grown but is the original fruit and ovule normally never or but very rarely to their full training: where one can assume that this disposition lies not from the lack of male fertilizing substance, but of one in the whole plant, a special education herrühre drive, which prevents <i>the development of plant</i>	375
1	Innere individuelle Verhältnisse und besondere Conceptionsfähigkeit einzelner Blumen eines Individuums, woraus sich allein die Erscheinung erklären lässt, dass unter (wenigstens dem Anschein nach) völlig gleicher Umständen, mit demselben Pollen, an demselben Individuum, bei gleicher Samenanlage, bei völlig <i>gleichem Entwicklungsgrade</i> und in demselben Momente der Bestäubung, die eine Blume eine grössere, die andere eine geringere Anzahl, ja! manche gar keine Samen geben.	Inside individual circumstances and special Conceptionsfähigkeit individual flowers of an individual, from which alone the phenomenon can be explained that under (at least apparently) completely the same circumstances, state of that pollen, the same individual, at the same ovule, with completely same <i>developmental state</i> and in To him moments of pollination, a flower, a larger, the other a smaller number, yes! give some no seeds.	375
1	Trockenheit, weil durch Feuchtigkeit sowohl die <i>Pollen Entwicklung</i> gehindert, als auch die Einsaugungsfunktion der Narbe unterdrückt wird.	Dry because moisture is prevented by both <i>pollen development</i> , as well as the Einsaugungsfunktion the scar is suppressed.	378
1	So beobachteten wir im Sommer 1839 ein im Topfe befindliches Exemplar des Verb. Blattaria, dessen erste	As we observed in the summer of 1839 a building under pots copy of the verb. Blattaria, the first and lowest three flowers were infertile,	380

	und unterste drei Blumen unfruchtbar waren, die vierte fruchtbar, die fünfte taub, die sechste bis dreiundzwanzigste fruchtbar, die vierundzwanzigste taub, die fünf-bis achtundzwanzigste fruchtbar, — nun folgten acht völlig taube Kelche, welche ohne alle <i>Blumen-Entwicklung</i> geblieben waren, — die siebenund achtunddreissigste taub, die neununddreissigste bis dreiundvierzigste fruchtbar, die vierundvierzigste bis sechsundsechzigste taub, die letzten und obersten drei Blumen wieder fruchtbar.	the fourth fertile, the fifth deaf, the sixth to twenty-third fertile, the twenty-fourth deaf, the five-to twenty-eighth fruitful, - now followed eight completely deaf chalice, which had remained without any <i>flower development</i> , - the thirty-eighth-seven deaf, the Thirty-ninth to forty-third fertile, the forty-fourth and sixty-sixth deaf, the last and highest three flowers fertile again.	
1	Manche Individuen der genannten Arten und viele, weniger fruchtbare Bastarde setzen auch gar keine Früchte und Samen mehr an ; sondern ihre Blumen verderben oder fallen ab, ohne nur eine Anregung zur <i>Entwicklung ihrer Fruchtknoten</i> gezeigt zu haben.	Some individuals of those species and many, less fertile hybrids also put no more on fruits and seeds; but its flowers perish or fall off, without showing only a suggestion to <i>the development of their ovaries</i> .	393
1	ohne <i>die mindeste Entwicklung der Ovarien</i> zu zeigen wie	without showing <i>the least development of the ovaries</i> as	395
1	Bei aller Unstätigkeit der Zeugungskraft der Bastarde ist es uns aber noch nicht gelungen, durch Cultur eine Veränderung <i>in der Entwicklung der Zeugungsorgane der Bastarde</i> wirken	In all Unstätigkeit the generative power of hybrids, however, we have not yet succeeded act by a culture alteration <i>in the development of the reproductive organs of hybrids</i>	395
2	Da jedoch das Zeugungsvermögen und die Fruchtbarkeit der Gewächse von <i>der Entwicklung der Geschlechtsorgane</i> abhängt, und die Umstände, welehe der <i>Entwicklung und Ausbildung</i> derselben in den sterilen	However, since the generation capacity and the fertility of the plants depends on <i>the development of the sex organs</i> , and the circumstance welehe to <i>shape and develop</i> the same Siehen in the sterile hybrids in ways still unknown: it must here	399

	Bastarden im Wege sehen, noch unbekannt sind: so müssen hierüber noch weitere Untersuchungen angestellt werden: wenn es gleich eine constatirte Thatsache ist, dass der Hybridismus der Fruchtbarkeit überhaupt hinderlich ist	about further research be conducted: if it is equal a constatirte fact is that the Hybridismus fertility is at all a hindrance	
1	Der Lychnicucubalus albus zeigte für sich selbst nicht <i>die geringste Entwicklung des Ovariums</i>	The Lychnicucubalus albus did not show for themselves the <i>slightest development of the ovary</i>	425
1	hatte für sich selbst nicht <i>die mindeste Entwicklung des Kelchs oder des Ovariums</i> gezeigt, diese sind vielmehr nach einigen Tagen verdorben	... had not shown itself for <i>the least development of the calyx or the ovary</i> , these are rather spoiled after a few days	426
2	es trat aber an den mit dem Pollen der L. syphilitica bestäubten Blumen ein <i>plötzlicher Stillstand der Entwicklung</i> ein, die Kelche wurden gelb und die Eichen hatten nicht <i>den geringsten Grad einer Entwicklung</i> erfahren: der Akt der Befruchtung scheint also hier zuerst auf die äusserste Umhüllung des Pistills gewirkt zu haben.	but it came to the dusty with pollen from flowers of L. syphilitica <i>a sudden stop of development</i> , which chalices were yellow and the oaks had not experienced <i>the slightest degree of development</i> : the act of fertilization seems here first on the outermost covering of the pestle to have worked.	426
1	Die Befruchtung unter gemischten Bastarden, oder auf diese Art entstandenen Varietäten, gibt keine gleichen Produkte: sondern es scheint ein unbestimmtes Wogen der beiden Befruchtungsthätigkeiten bei Erzeugung der Keime obzuwalen, wodurch in Einer Befruchtung und <i>in Einem Ovarium Keime mit verschiedenen Entwicklungsformen</i> gebildet werden	The fertilization mixed hybrids, or on this kind incurred varieties are no identical products: but it seems a vague waves of the two Befruchtungsthätigkeiten upon generation of germs obzuwalen, which are formed in one insemination and <i>in one ovary nuclei with different forms of development</i>	428
1	Die Bastardpflanzen also,	The Bastard plants so that should	458

	<p>welche zu diesem Umwandlungsversuche dienen sollen, müssen nothwendig noch einen gewissen Grad weiblichen Conceptionsvermögens besitzen: so dass, wenn sie auch für sich selbst unfruchtbar oder ihr Pollen impotent sein sollte; doch der stammelterliche Befruchtungsstoff noch eine Befruchtung bewirken kann, welcher dann bei der künstlichen Bestäubung und der Schwangerung der hybriden Eichen keinen anderen Einfluss zulässt und die Richtung bestimmt, welche <i>die Entwicklung des hiedurch erzeugten Embryos</i> bei den aus diesen Samen entstandenen Samlingen nehmen muss.</p>	<p>serve this Umwandlungsversuche must necessarily still have a certain degree female Conceptionsvermögens: so that if they should be impotent for themselves infertile or their pollen; but the derived parental fertilization fabric still can cause fertilization, which then does not allow any other influence in artificial pollination and the Swan Gerung the hybrid oaks and the direction is determined, which must take <i>the development of the embryo</i> by this means generated in the seedlings resulting from these seeds.</p>	
1	<p>Die Versuche sind nur in Reihe von Jahren zu bewerkstelligen und zu beendigen; weil in dem langsamen Verlauf der Zeugungen und in dem langen Hin-Ziehen <i>der Entwicklungen</i> sowohl, als durch die verschiedenen Fruehtbarkeitszustände der Yersuchs-Individuen sehr leicht und oft Störungen und Ausfälle eintreten können, welche das begonnene Werk unterbrechen und, wenn es noch gut geht, das Resultat um einen Jahrs-Cyclus hinausschieben.</p>	<p>The experiments are accomplished only in number of years and quit; because in the slow course of the beliefs and in the long round pulling <i>the developments</i> both, very easily and often can occur faults and failures through the various Fruehtbarkeitszustände the Yersuchs individuals, which interrupt the work begun and if it still goes well, the result postpone a year-cycle.</p>	476
1	<p>Der Verf. legt ein besonderes Gewicht für eine solche Umwandlung darauf, dass das Thlaspi <i>in allen seinen Entwicklungsstufen</i> mit dem Reps parallel gehe.</p>	<p>The author. Places particular emphasis for such Umwandlung that the Thlaspi in <i>all its stages of development</i> with the Reps go parallel.</p>	487
1	<p>die 15te zeigte aber schon beim Keimen Verschiedenheiten,</p>	<p>But the 15th already showed differences in germination, and a</p>	488

	und <i>eine langsame Entwicklung</i> und kränkelnde Beschaffenheit.	<i>slow development</i> and ailing condition.	
1	<i>Während ihrer Entwicklung</i> glichen diese Knospen selbst in Hinsicht der weissen Farbe der Blumenblätter, mit Ausnahme ihrer doppelten Grösse, ganz denen des <i>Thlaspi arvense</i> .	<i>During their development</i> , these buds aligned itself in terms of the white color of the petals, with the exception of double size, all of which <i>Thlaspi arvense</i> .	488
1	Der Verf. ist geneigt mit Thaer das <i>Trifolium fragiferum</i> für eine Varietät des <i>T. repens</i> zu halten, dass sich das erstere nur <i>auf einer niederen Stufe der Entwicklung</i> befinde, und dass sein Erscheinen ursprünglich durch Bodenverhältnisse bedingt werde.	The author is. Inclined to keep with the Thaer <i>Trifolium fragiferum</i> for a variety of <i>T. repens</i> , that the former is located only <i>at a lower stage of development</i> , and that his appearance would originally due to soil conditions.	493
3	Werde dieses ursprüngliche, die <i>vollständige Entwicklung</i> , ja die Existenz der Art bedingende, Verhältniss aufgehoben, so sei die Abweichung einer Pflanze von ihrem Normaltypus die nothwendige Folge davon , d. i. <i>die Entwicklung und Bildung einer jeden Pflanze beruhe auf gewissen Gesetzen</i> , und werde durch diese bedingt, und diese Gesetze sprechen sich aus in den, zur <i>vollkommenen Entwicklung einer Pflanze</i> nothigen, verschiedenen Verhältnissen der Einwirkung der ausseren Momente, Licht, Feuchtigkeit, Boden, Luftbeschaffenheit, Wärme u. s. w. Noch kennen wir freilich diese Gesetze so gut als gar nicht; ihr Vorhandensein lasse sich aber durchaus nicht mehr verkennen, wir seien vielmehr durch eine Menge von Erscheinungen gezwungen, sie als vorhanden anzunehmen.	Get this original, <i>full development</i> , so the existence of the species conditional, Relationship repealed, the deviation of a plant from its normal type is the necessary consequence of which, ie <i>the development and formation of each plant based on certain laws</i> , and will due to this, and these laws are in favor of the, nothigen to <i>the perfect development of a plant</i> , different ratios of exposure to the outer moments, light, moisture, soil, air quality, heat etc Yet we certainly know these laws as well as not; but their presence is by no means let more mistaken, we are forced rather by a set of phenomena, to accept them as yet.	494
1	Nur gewissen bestimmten	Only certain specific families is	495

	Familien sei eine solche eigen, und diese seien solche, welche <i>die niederen Entwicklungsstufen des Pflanzenreichs</i> überhaupt, oder einer Familie, oder endlich einer Gattung darstellen, in welcher die Einheit noch nicht zur Vollkommenheit gelangt sei, um sich gegen die veränderten äusseren Verhältnisse in ihrer Integrität zu behaupten, und diese gleichsam überwinden zu können,	such a self, and these were those which <i>at all the lower stages of development of the plant kingdom</i> , or a family, or finally constitute a genre in which the unit had not yet reached that perfection to stand up to the changing external conditions to maintain in their integrity, and to overcome this, as it can be,	
1	Die gewöhnlichen kleinen Linsen, unter welchen die Kichern sich befunden hatten, blieben <i>in ihrer ganzen Entwicklung</i> ganz unverändert.	he common small lenses, under which the giggles had been had remained completely unchanged <i>in its whole development</i> .	497
1	der Limbus <i>im Anfang der Entwicklung der Blumen</i> schmal und mehr gerundet mit leichter Andeutung der Lappenspitzen, die Lappen mehr nur angedeutet, als unterschieden	the limbus <i>in the early development of the flowers</i> small and more rounded with a slight hint of rag tops, the lobes longer just indicated, as distinguished	512
1	Bei <i>der weiteren Entwicklung der Pflanzen</i> und beim vollendeten Wachstum zeigten sich die später entwickelten Blumen noch weniger von denen der <i>N. angustifolia</i> verschieden	<i>In the further development of the plant</i> and the completed growth of the later-developed flowers showed even less differen from those of <i>N. angustifolia</i>	512
1	Aber eine hieherbezügliche, im Jahr 1826 veranstaltete, Bestäubung des Bastards <i>Nicoliana rustico-paniculata</i> mit dem Pollen des <i>Hyoscyamus agrestis</i> haben wir noch besonders beizufügen, dass von 6 Befruchtungen zwei angeschlagen zu haben schienen; indem zwei kleine Früchte mit je zwei vollkommenen Samen erhalten	But a hieherbezügliche, organized in 1826, pollination of Bastards <i>Nico Liana Rustico-paniculata</i> with the pollen of <i>Hyoscyamus agrestis</i> we do not have particularly accompanied to have that posted by 6 inseminations two rails; by two small fruits were obtained with two perfect seeds, which have however only two germinated, and only one plant has come to <i>a complete development</i> .	314

	wurden, wovon jedoch nur zwei gekeimt haben, und nur eine einzige Pflanze zur <i>völligen Entwicklung</i> gekommen ist.		
1	Ebenso auch die <i>Blumenentwicklung</i> .	The <i>flower-development</i>	518
1	indem Eigenschaften, welche bei den Hybriden angetroffen werden, auch bei den reinen Arten durch <i>alterirte Entwicklung</i> hervorgebracht werden:	by properties which are encountered in the hybrids are produced by <i>altered development</i> even in the pure species:	518
2	sondern, dass ein grosser, ja der grosste Theil derselben <i>in verschiedenen Graden der Entwicklung</i> stehen geblieben ist (s. oben Unvollkommene Befruchtung S. 93), obgleich im sonstigen Gang und der Entwicklung der Früchte, selbst in der Reifungszeit der Samen vielfältig kerne Abweichung zu bemerken ist.	but that a large, indeed the biggest part has remained the same are <i>in different degrees of development</i> (see Fig. above imperfect fertilization p 93), although to notice diverse cores deviation in other transition and the development of the fruit, even in time of ripening of the seeds is.	519
1	Bei noch andern setzt sich, wenn auch die erste Entwicklung kein Hinderniss gefunden hat, das Siechthum der Samlinge fort; sie treiben zwar Aesle und Blätter, können aber nicht zur <i>Entwicklung der Blumen</i> gelangen, oder wenn sie auch bei besonders günstiger Witterung solche ansetzen	In yet another set when the first development has found no obstacle, the infirmity of the seedlings continued; Although they drive Aesle and leaves, but can not get to <i>the development of the flowers</i> , or if they fix those even in the most favorable weather	520
1	Vielleicht mögen auch äussere Einflüsse zum Siechthum mehrerer dieser Bastarde Veranlassung gegeben haben: wie wir dann auch an dem Verbascum Thapso-phoeniceum in dem nassen und kühlen Sommer von 1831 zwar Blätter, Stengel und Aeste treiben, aber keine Blumen zur <i>Entwicklung</i> kommen sahen.	Maybe external influences to infirmity more of these bastards may have given rise: as we also to the Verbascum Thapso-phoeniceum in the wet and cool summer of 1831, although leaves, stems and branches drive, but saw no flowers come for <i>development</i> .	520
1	Aber nur wenige Samen	But few seeds seem to find in their	525

	scheinen in ihrer natürlichen Anlage eine Veränderung durch die Verzögerung ihres Keimens zu erfahren, wir kennen nur die Melonen, Gurken und Kürbisse, welche <i>in der Entwicklung der Sexualorgane</i> durch das Aufschieben des Keimens der Samen eine andere Richtung bekommen (s. oben S. 370).	natural plant an alteration by the delay of its germination, we only know the melons, cucumbers and pumpkins, which get <i>in the development of the sexual organs</i> by pushing the germination of seeds a different direction (see Fig. Above p 370).	
1	Eine der ausgezeichnetsten und allgemeinsten Eigenschaften; der Pflanzenbastarde ist die Luxuriation in allen ihren Theilen indem sich bei sehr vielen derselben eine Ueppigkeit <i>des Wachstums und der Entwicklung von Wurzelschossen, Aesten, Blättern und Blumen</i> zeigt, welche bei den Stammeltern auch bei sorgfältiger Cultur nicht angetroffen wird	One of the highest and most general properties; plant hybrids is the Luxuriation in all its parts by themselves in very many of the same shows a luxuriance of <i>growth and development of root stem elongation</i> , branches, leaves and flowers, which is not encountered in the first parents, even with careful cultivation	526
1	Gewöhnlich erlangen aber die Bastardpflanzen nur im freien Boden <i>die vollkommene Entwicklung ihrer Theile</i> , wie schon Kolreuter bemerkt hat:	But usually get the bastard plants only in the free soil <i>the perfect development of their parts</i> , as has been noted Kolreuter	526
1	Die verschiedenen Bastarde von Datura ... wachsen zu grossen umfangreichen Baumen aus, deren Aeste und Blätter die Stämme beinahe niederdrücken, ohne noch zur <i>Entwicklung ihrer unzähligen Blumen</i> gelangt zu sein.	The various hybrids of Datura ... grow into big bulky trees, whose branches and leaves almost depress the tribe, but not yet attained to <i>the development of their innumerable flowers</i> .	527
1	Ist die Luxuriation in dem hybriden Pflanzenkörper schon vor <i>der Entwicklung der Blüthe</i> sichtbar und vorhanden	Is the Luxuriation in the hybrid plant body even before <i>the development of the flower</i> visible and available	528
1	Beschleunigung und Vermehrung der <i>Blumenentwicklung</i> .	Acceleration and propagation of <i>flower-development</i>	529
1	Mit dem beschleunigten und erhöhten <i>Wachsthum und der frühen Entwicklung des hybriden Pflanzenkörpers</i> steht	With the accelerated and increased <i>growth and early development of the hybrid plant body</i> is the earlier flowering of hybrids in the closest	530

	das frühere Blühen der Bastarde in der engsten Verbindung.	connection.	
1	Kolreuter ist geneigt, den Grund des früheren Blühens und der fortdauernden zahlreichen <i>Blumenentwicklung</i> ebenfalls in der Unfruchtbarkeit der Bastarde zu suchen; weil diese Eigenschaften bei den im höchsten Grade unfruchtbaren Hybriden in einem vorzüglich hohen Grade angetroffen werden.	Kolreuter is inclined also to seek the reason for the earlier flowering and the continuing numerous <i>flower-development</i> in the sterility of hybrids; because these properties are encountered in the unfruitful in the highest degree hybrids in an excellent high grade.	532
1	Die Luxuriation der Bastarde, die Productivity in Blumen und ihre längere Dauer konnte man dem Mangel <i>der Entwicklung und Verstaubung des Pollens</i> zuschreiben	The Luxuriation the hybrids whose productivity in flowers and their Longer duration could be attributed to the lack of <i>development and dusting of pollen</i>	533
1	Abends gegen 5 Uhr (im Juni) begann aber die <i>Geruchsentwicklung</i> und stieg bis gegen Mitternacht	In the evening around 5 clock (in June) but <i>odor began developing</i> and rose up around midnight	536
1	es setzten bios rudimentäre Kapseln an, mit staubartig vertrockneten Eichen, und keines derselben zeigte nur einen Schein von <i>einiger Entwicklung</i>	it sat bios rudimentary capsules at, with dust-like withered oaks, and none of them showed only a semblance of <i>some development</i>	539
1	das dritte Exemplar dauerte fünf Jahre und trieb die gleichen gebänderten Triebe aus der Wurzel, an welchen jedoch, wie am Hauptstamm, niemals eine Blume zur <i>Entwicklung</i> gekommen ist	the third copy took five years and drove the same banded shoots from the root, to which, however, as the main stem, never a flower has come for <i>development</i>	560
1	die Corollen kamen durch die Luxuriation und Krümmung der Staubfäden und die unförmlichen Antheren nicht zur <i>regelmässigen Entwicklung</i> , sondern wurden in röthlich-grüne, filamentartige Lacinien getheilt und mit den kraus in einander	the corollas came through the Luxuriation and curvature of the stamens and anthers shapeless not for <i>regular development</i> , Segregate were divided into reddish-green, filamentous Lacinien and presumably grow with the frizzy tangled in each other stamens	562

	verschlungenen Staubgefäßen verm wachsen		
1	An vier Pflanzen dieser Art, welche aus dem gleichen Samen aus einer und derselben Schote aufgegangen waren, wurden alle Blumenknöpfe vor <i>ihrer Entwicklung und eingetretenen Reife der Antheren</i> zu gleicher Zeit castrirt	At four plants of this species, which had gone up from the same seed from one and the same pod, all flowers buttons were castrated before <i>their development and maturity of the anthers</i> occurred at the same time	566
2	Das Alter der Samen hat nach dem Zeugniß vieler bewährten Blumisten (s. oben S. 92) einen wesentlichen Einfluss, bei <i>der Geschlechtsentwicklung</i> bei den Dichogamen (s. oben S. 370), so auch auf <i>die Entwicklung der Füllung der Blumen</i> bei mehreren Pflanzen, namentlich den Levcojen, Balsaminen und Nelken nach Huffner Rossnagel, Lecoq und FÜRST	The age of the seeds after the testimony of many has proven Blumisten (see Fig. Above, p 92) has a significant influence on <i>the development of sex</i> at the Dichogamen (see Fig. Above S. 370), as well as on <i>the development of the filling of the flowers</i> on several plants, namely the Levcojen, balsams and cloves after Huffner Rossnagel, Lecoq and FÜRST	567
1	Nur wenige Blumen der <i>Lychnis diurnoflos cuculi</i> (s. oben S. 50, 105, 348) kamen zu <i>ihrer vollkommenen Entwicklung</i>	Only a few flowers of <i>Lychnis diurnoflos cuculi</i> (see Fig. Above, p 50, 105, 348) came to <i>their perfect development</i>	570
1	Kelch und Corolle waren noch weit <i>in der Entwicklung</i> zurück.	Calyx and corolla were far back <i>in the development</i> .	570
1	Es ist ersichtlich, dass diese Auswüchse rait andern an reinen Arten nicht selten vorkommenden übereinkommen, und nichts Aussergewöhnliches darbieten, deren häufigere <i>Entwicklung aber der Luxuriation der Hybriden</i> in diesem Falle beizumessen sein dürfte.	It can be seen that these excesses rait other to pure species agree not rare, and nothing unusual present, the more frequent <i>development of luxuriance of the hybrids</i> is likely to be accorded in this case.	571
3	Die Hemmung und der Mangel der Frucht- und Samenbildung scheint hier nur durch die beschleunigte Erzeugung und das gesteigerte Hervorsprossen einer fast unendlichen Menge	The inhibition and the lack of the formation of fruit and seed appears here only by the accelerated production and increased emphasis sprouts an almost infinite amount voa	572

	<p>voa Blumen, und die langere Dauer <i>dieser Entwicklung</i> ersetzt zu werden. Die <i>allgemeinen Entwicklungsgesetze der Theile der Gewächse</i> scheinen daher durch die Irybride Zeugung keine, den Sinnen perceptible Aenderung zu erfahren; sondern alle <i>Entwickelungen und Veränderungen des hybriden Pflanzenkörpers</i> nach denselben Gesetzen zu erfolgen, wie bei den reinen Arten; die Zeugungsorgane und die ateriellen Grundstoffe der Zeugung allein ausgenommen.</p>	<p>flowers, and the Longer duration of <i>this development</i> to be replaced. <i>The general law of development of the parts of the plants</i> therefore appear by the Irybride generation to learn no, the senses perceptible change; but to be made all <i>changes and developments of the hybrid plant body</i> according to the same laws as the pure species; the reproductive organs and the ateriellen Raw materials of procreation alone excepted.</p>	
1	<p>so scheint es unerklarlich zu sein, warum die Corolle bei den absolut sterilen Bastarden, deren es doch sehr viele gibt, keine Störung oder Beschleunigung <i>in ihrer Entwicklung oder Bildung</i> erfahrt;</p>	<p>it seems to be inexplicable why the corolla at the absolutely sterile hybrids, of which there are still very many, no disturbance or acceleration learn <i>in their development or formation</i></p>	572
1	<p>besonders können von Seiten der männlichen Organe alle die Umstände die Bastardzeugung begünstigen und die Fremdbestäubung erleichtern, welche <i>ihrer zeitgemässen Entwicklung</i> im Wege stehen, z. B. anhaltender Regen, feuchte und kalte Witterung, heftige Winde, allzugrosse und anhaltende Sonnenhitze, welche atmosphärische Einflüsse das Oeffnen der Staubbeutel hindern, den Pollen verderben oder unkräftig machen</p>	<p>particularly to the part of the male organs of all the circumstances favor the bastard procreation and facilitate the cross-pollination, which <i>their current development</i> in the way of such. B. and rainy, wet and cold weather, strong winds, too large and persistent heat of the sun, which atmospheric influences the opening of the anthers prevent the pollen from spoiling and weakening</p>	585
1	<p>Bei den weiblichen Organen aber kann ihre nicht seiten vorkommende <i>frühzeitige Entwicklung</i> und das</p>	<p>But in the female organs can not part their effect occurring <i>early development</i> and the emergence penetrating</p>	585

	Hervordringen der Narbe aus der noch enggeschlossenen Blumenknospe und ihre hiedurch möglich gewordene Bestäubung durch, auf verschiedene Weise hergeführten, Pollen zur Zeit ihrer Conceptionsfähigkeit eine Bastardbefruchtung im Freien bewirken	the stigma from the still tightly closed flower bud and its By this means become possible through pollination, hergeführten in various ways, pollen at the time of their Conceptionsfähigkeit a hybridisation outdoors	
1	4) durch <i>das Gesetz der Gleichzeitigkeit der Entwicklung der beiderlei Befruchtungsorgane in einer Blume</i>	4) by <i>the law of the simultaneity of the development of both reproductive organs in a flower</i>	586
1	es ist also derjenige Theil in dieser heterogenen Verbindung, welcher mit seinem Saft nach Quali- und Quantität die Emte oder das aufgesetzte Auge ernähert, und also den ersten und stärksten Einfluss auf <i>das Wachsthum und die weitere Entwicklung der aufgesetzten Knospe</i> haben muss	So it is that part in this heterogeneous connection, which ernähert the Emte or the patched eye with its juice according to quality and quantity, and therefore must have the first and strongest influence on <i>the growth and further development of the patch bud</i>	607
1	über die weitere Folge <i>der Entwicklung der Emte ihrer Blätter und Früchte</i> u. s. w. ist aber in der Beschreibung kein genauer Bericht gegeben.	etc. on the further consequence of <i>the development of Emte of their leaves and fruits</i> but is given in the description of an exact report.	618
1	Für die Blumencultur ist die grosse Ausbreitung und gigantische Grösse, welche manche Bastarde entwickeln, z. B. von den Gattungen Verbascum, Lobelia, Digitalis, Althaea, Lavatera, Malva Datura, Mirabilis u. s. w. und die damit verbundene unerschöpfliche <i>Entwicklung von Blumen</i> ein nicht unbedeutender Gewinn	For the Blumencultur is the large spread and gigantic size, which develop some hybrids, z. Example of the genus Verbascum, Lobelia, digitalis, Althaea, Lavatera, Malva Datura, Mirabilis, etc and the associated inexhaustible <i>development of flowers</i> a not insignificant profit	643
1	Dass Alles dieses, sowie die Verhütung der Verwechselung und die Pflege der Samlinge in dem mehr als gewöhnliche	That all this, and the prevention of confusion and the care of the seedlings in the more than ordinary further course of <i>their</i>	649

	ferneren Verlauf <i>ihrer Entwicklung</i> eine Aufmerksamkeit und Ausdauer erfordert, liegt wohl am Tage	<i>development</i> requires attention and perseverance, is probably the day	
1	es ist noch das Keimen der Samen, <i>die Entwicklung der Bastardsämlinge abzuwarten und ihr Fruchtbarkeitszustand</i> , ihre Dauer u, s. w. zu beobachten	it is still the germination of seeds, <i>await the development of the seedlings of hybrid and their fertility status</i> , duration, & c observed	650
1	Durch dieses strenge und, wenn man will, minutiöse Verfahren gewann aber der Verf. den grossen Vortheil, dass er seine Pfleglinge und jede einzelne Hybride <i>während ihrer Entstehung, Entwicklung und ihrer ganzen Lebensdauer</i> keinen Augenblick aus den Augen verlor:	Through this rigorous and, if you will, meticulous process but won the author the great advantage that <i>during their formation, development and all its life</i> , he lost his Pfleglinge and each hybrid for a moment from his eyes.:	651
1	um die Vegetation und <i>die weitere Entwicklung dieser Pflanzen</i> nicht zu unterbrechen oder zu storen	to the vegetation and <i>the further development of these plants</i> not to interrupt or interfere	662
1	sondern auch weil <i>die Entwicklung aller Theile der Blume</i> durch ihre Einwirkung sehr begünstigt wird	but also because <i>the development of all parts of the flower</i> is very favored by their action	665
1	Die wirklichen Bastardpflanzen erlangen zwar im freien Lande gewöhnlich <i>eine vollkommenere Entwicklung</i> , und zeigen ein üppigeres Wachsthum des Stammes, der Aeste und der Blätter und erzeugen daher auch eine viel grössere Anzahl von Blumen, welche gemeiniglich aber alle unbefruchtet bleiben oder abfallen:	The real hybrid plants become true in the open ground usually <i>a more perfect development</i> , and show a more luxuriant growth of the trunk, the branches and leaves, and therefore also generate a much larger number of flowers, which commonly but all remain unfertilized or fall:	667
1	Andererseits haben wir aber auch in einzelnen Fällen unseren Zweck dadurch erreicht, dass wir <i>die Blütenentwicklung</i> der späteren Art durch die Stellung der Pflanzen in eine wärmere	On the other hand, we have achieved in individual cases our purpose, we accelerated <i>the flower-development</i> the later type by the position of the plants in a warmer location,	668

	Lage beschleunigt,		
1	oder die Blumen mit reinem besprengt, wodurch <i>die Entwicklung der Antheren</i> ohne Nachtheil für die Kraft des Befruchtungsstoffs,	or the flowers sprinkled with pure, whereby <i>the development of the anthers</i> without disadvantage for the power of the fertilization substance,	668
2	War aber das eine oder das andere Individuum der zu verbindenden Arten <i>in der Entwicklung seiner Blumen und Sexualorgane</i> um Etwas zurück: so setzten wir die betreffende Pflanze im Topfe einer kräftigen Einwirkung des Sonnenlichts und der Wärme aus, wodurch <i>die Entwicklung des einen oder des anderen Befruchtungsorgans</i> befördert wurde.	But it was one or the other individual of the species to be joined <i>in the development of his flowers and sexual organs</i> to something back: so we put the question plant in the pot a strong influence of the sunlight and the heat out, making <i>the development of one or the other fertilization organ</i> was promoted.	669
1	Durch die zweckmassige Anwendung dieser Mittel waren wir im Stande, <i>die Entwicklung der Zeugungsorgane</i> einander näher zu bringen: um zur geeigneten Zeit die Fremdbestäubung zu vollbringen und manche Versuche auszuführen, welche ohne dieselben nicht hätten ausgeführt werden können.	Were assigned by the massive application of this means we able to bring <i>the development of the organs of generation</i> closer: at the appropriate time to perform the cross-pollination and carry out some experiments which could not have been without them can be performed.	669
1	Bei allen Versuchen des Verf. und bei der Pflege seiner Versuchs -Exemplare war aber zugleich seine Sorge stets dahin gerichtet, dass dadurch <i>der natürliche Gang ihrer Entwicklung und ihres Wachstums</i> nicht gehindert oder unterbrochen wurde.	In all experiments, the Author., And in the care of his trial copies shall at the same time but was always addressed his concern as meaning that characterized <i>the natural course of their development and their growth</i> was not prevented or interrupted.	670
1	so ist es nothwendig, <i>die vollständige Entwicklung der Pflanzen</i> aus den ausgesaten Samen abzuwarten, welche erst die völlige Gewissheit geben können, dass eine Bastardzeugung und keine	so it is necessary to wait for <i>the full development of the plants</i> from the seeds ausgesaten, which only can give the complete certainty that a hybrid procreation and no after fertilization was done, as well as Herbert W.	674

	Afterbefruchtung geschehen war, wie auch W. Herbert		
1	Eine weitere Aufgabe ist es, die Sämlinge aus diesen Aussaaten Alle, so viel es ihrer sind, zu erhalten und zur <i>vollkommenen Entwicklung</i> zu bringen und abgesondert zu erziehen, um über die Typen und ihre Gleichförmigkeit oder Ungleichheit in Gewissheit zu kommen	A further object is to get the seedlings from these sowings all, so much as they are, and to bring to <i>the perfect development</i> and selected to educate, to come upon the types and their uniformity or inequality in certainty	675
1	Wenn nun aber auch mit <i>der vollständigen Entwicklung der Bastardpflanzen</i> der Hauptzweck unserer Versuche erreicht war: so waren erst noch die einzelnen Pflanzen jeder Art in Beziehung auf den Zustand ihrer Befruchtungsorgane und ihrer Fruchtbarkeit zu untersuchen: was nicht nur in physiologischer Beziehung überhaupt von Wichtigkeit, sondern auch in praktischer Hinsicht für die Umwandlung zu wissen nöthig war.	When was now but also of <i>the complete development of hybrid plants</i> , the main purpose of our experiments achieved so were only nor the individual plants of each kind to examine in relation to the state of their reproductive organs and fertility: what not only in physiological relationship at all of importance, but was to know in practical terms for the Umwandlung necessary.	675
2	Es steht nun zu erwarten: 1) ob dieselben Wurzeln im zweiten Trieb (1849) wieder ebensolche verschiedene Samen erzeugen werden, als aus <i>der ersten Entwicklung</i> hervorgingen. 2) Wie sich diese verschiedenen Samen <i>in ihrer weiteren Entwicklung</i> (im Jahr 1849) in Absicht auf den Typus der Pflanzen und ihrer Samenerzeugung verhalten werden.	It is now expected to: 1) whether the same roots in the second train (1849) will again produce just such different seeds, as emerged from <i>the first development</i> . 2) How do these various seeds <i>in their further development</i> will behave in intent to the type of plants and their seed production in 1849.	679-680
1	6) Bezeichnet (mit H) <i>die vollständige Entwicklung des Bastards</i> und seine Aufnahme in die Sammlung: der Beisatz (Ic.) bedeutet die Abbildung desselben im Ganzen oder nur	6) Identifies (with H) <i>the full development of the hybrids</i> and its inclusion in the collection: the garnish (. Ic) is the image of the same in whole or in flower.	681

	in der Blume.		
1	Lee re Befruchtung: Die Corolle fällt bald ab ⁵ oder verdirbt, der Kelch und der Fruchtknoten wachsen ein wenig, die Eichen aber erfahren <i>keine Entwicklung</i> , womit vollkommene Unfruchtbarkeit stattfindet.	Lee re-fertilization: the corolla falls soon AB ⁵ or spoils, the calyx and the ovary grow a little, but the oaks undergone <i>any development</i> , thus perfect infertility occurs.	681
1	Mangelhafte Befruchtung: Der Zustand der Blumenkrone und des Kelches wie bei c), die ausseren Fruchthüllen zuweilen ziemlich ausgebildet mit <i>einiger Entwicklung der Eichen</i> in ihren Umhüllungen	Poor fertilization: The state of the corolla and the calyx as in c), the outer fruit servings sometimes quite formed with <i>some development of the oaks</i> in their enclosures	681
1	Vollkommene Befruchtung: Die Früchte meistens vollkommen, doch auch häufig klein und mager, mit alien Graden und <i>Formen der Entwicklung hybrider Samen</i> , und wenigen, ja! zuweilen nur einem einzigen oder ein paar keimungsfähigen, vollkommenen Samen.	Perfect fertilization: The fruits usually perfect, but too often short and thin, with alien forms and <i>degrees of development of hybrid seeds</i> , and a few, yes! sometimes only one or a few keimungsfähigen, perfect seeds.	682
1	der Pollen des Cucubalus viscosus bewirkt dagegen <i>eine normale Entwicklung des Pericarps</i> mit vielen vertrockneten Eichen, vielen eckigen, eingeschrumpften Samenbalgen und einigen wenigen guten Samen:	the pollen of Cucubalus viscosus in contrast, causes <i>a normal development of the pericarp</i> with many withered oaks, many angular, shrunken seeds bellows and a few good seeds:	684
1	Die Bestäubung der Lychnis diurna mit dem Pollen der Saponaria officinalis, Silene bellidifolia und Lychnanthus volubilis bewirkte <i>gar keine Entwicklung des Pericarps</i> , sondern hatte eine tödtliche Wirku auf die ganze Blume.(S. oben Pollenwirkung.)	The pollination of Lychnis diurna with the pollen of Saponaria officinalis, Silene bellidifolia and Lychnanthus volubilis caused <i>no development of the pericarp</i> , but had a tödtliche Wirku on the whole flower. (S. Above pollen effect.)	684

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